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XVII CONGRESSUS INTERNATIONALIS ORNITHOLOGICUS

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XVII CONGRESSUS INTERNATIONALIS ORNITHOLOGICI

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HERAUSGEGEBEN VON

ROLF NÖHRING

BAND I

VERLAG DER DEUTSCHEN ORNITHOLOGEN-GESELLSCHAFT

BERLIN 1980

Die Vignette, die auch als Kongreßabzeichen diente, stellt einen Hahn
der Großtrappe *Otis tarda* zu Beginn der Balzhandlungen dar.
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DIE INTERNATIONALEN ORNITHOLOGEN-KONGRESSE 1884—1978

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I	Vienna	1884	Dr. G. F. R. Radde	Dr. Gustav von Hayek
II	Budapest	1891	Prof. Victor Fatio und Otto Herman	—
III	Paris	1900	Dr. Émile Oustalet	Jean de Claybrooke
IV	London	1905	R. Bowdler Sharpe	Dr. E. J. O. Hartert J. Lewis Bonhote
V	Berlin	1910	Prof. Dr. Anton Reichenow	Herman Schalow
VI	Copenhagen	1926	Dr. E. J. O. Hartert	E. Lehn Schiøler
VII	Amsterdam	1930	Prof. Dr. A. J. E. Lönnberg	Prof. Dr. L. F. de Beaufort
VIII	Oxford	1934	Prof. Dr. Erwin Stresemann	Rev. F. C. R. Jourdain
IX	Rouen	1938	Prof. Alessandro Ghigi	Jean Delacour
X	Uppsala	1950	Dr. Alexander Wetmore	Prof. Dr. Sven Hörstadius
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XII	Helsinki	1958	Prof. J. Berlioz	Dr. Lars von Haartman
XIII	Ithaca	1962	Dr. Ernst Mayr	Dr. Charles G. Sibley
XIV	Oxford	1966	Dr. David Lack	Prof. Dr. N. Tinbergen
XV	Den Haag	1970	Prof. Dr. Nikolaas Tinbergen, 1966—1969 Prof. Dr. Finn Salomonsen, 1969—1970	Prof. Dr. Karel H. Voous
XVI	Canberra	1974	Prof. Dr. Jean Dorst	Dr. H. J. Frith
XVII	Berlin	1978	Prof. Dr. D. S. Farner	Rolf Nöhring

VERZEICHNIS DER FRÜHEREN KONGRESSBERICHTE

I. Sitzungs-Protokolle des ersten Internationalen Ornithologen-Congresses, der vom 7. bis 11. April 1884 in Wien abgehalten wurde. Wien, Verlag des Ornithologischen Vereines in Wien, 1884. vi + [90] p.

Mitteilungen des Ornithologischen Vereins Wien, Band viii-x, 1884—86.

II. Bericht ... Zweiter Internationaler Ornithologischer Congress, Budapest, 1892. (Blasius) [n.p.; 1891] 58 p.

III. IIIe Congrès Ornithologique international, Paris/26—30 juin 1900. Compte rendu des séances publié par É. Oustalet ... et J. de Claybrooke ... Masson et Cie, Paris. xii + 503 p. 1901. [= Ornis, vol. 11]

IV. Proceedings of the Fourth International Ornithological Congress, London/June 1905. Edited by R. B. Sharpe, E. J. O. Hartert, and J. L. Bonhote. Dulau & Co., London. 696 p. 1907. [= Ornis, vol. 14]

V. Verhandlungen des V. Internationaler Ornithologen-Kongresses, Berlin 30. Mai bis 4. Juni 1910. Herausgegeben von Herman Schalow ... Deutsche Ornithologische Gesellschaft, Berlin. x + 1186 p. 1911.

VI. Verhandlungen des VI. Internationalen Ornithologen-Kongresses in Kopenhagen, 1926. Herausgegeben von Dr. F. Steinbacher. Berlin. vi + 641 p. 1929.

VII. Proceedings of the VIIth International Ornithological Congress at Amsterdam. Amsterdam. vii + 527 p. 1931.

VIII. Proceedings of the Eighth International Ornithological Congress/Oxford/July 1934. Edited by F. C. R. Jourdain. Oxford University Press, Oxford. x + 761 p. 1938.

IX. IXe Congrès Ornithologique International/Rouen—9 Au 13 Mai 1938. Compte Rendu publié par Jean Delacour ... Rouen. 543 p. 1938.

X. Proceedings of the Xth International Ornithological Congress/Uppsala/June 1950. Edited by Sven Hörstadius. Almqvist & Wiksells, Uppsala. 662 p. 1951.

XI. Acta XI Congressus Internationalis Ornithologici/Basel 29. V.—5. VI. 1954. Herausgegeben von Adolf Portmann und Ernst Sutter. Birkhäuser Verlag, Basel und Stuttgart. 680 p. 1955.

XII. Proceedings/XII International Ornithological Congress/Helsinki. 5.—12. VI. 1958. Edited by G. Bergman, K. O. Donner, L. v. Haartman. Tilgmannin Kirjapaino, Helsinki. 2 vol. 820 p. 1960.

XIII. Proceedings XIII International Ornithological Congress/Ithaca 17—24 June 1962, Editor: Charles G. Sibley. Published by The Ornithologist's Union, Baton Rouge, Lousiana. 2 vol. xvi + 1246 p. 1963.

XIV. Proceedings of the XIV International Ornithological Congress/Oxford 24—30 July 1966. Edited by D. W. Snow. Blackwell Scientific Publications, Oxford and Edinburgh. xxiv + 405 p. 1967.

XV. Proceedings of the XVth International Ornithological Congress/The Hague 30 August—5 September 1970. Edited by K. H. Voous. E. J. Brill, Leiden. viii + 745 p. 1972.

XVI. Proceedings of the 16th International Ornithological Congress/Canberra 12—17 August 1974. Edited by H. J. Frith and J. H. Calaby. Australian Academy of Science, Canberra. xviii + 765 p. 1976.

Zu diesem Bande

Die beiden Bände über die Verhandlungen des Ornithologenkongresses, die ich hier vorlege, tragen einen lateinischen Titel, mit dem der internationale Charakter dieser Veröffentlichung unterstrichen werden soll. Gemäß dem Sprachgebrauch der Gastgeber ist der Bericht über die Vorbereitungen und den Verlauf des Kongresses deutsch abgefaßt. Der allgemeine Teil ist, wo notwendig, mit englischen Untertiteln versehen, die Vorträge und Kurzfassungen sind in der Sprache wiedergegeben, die der jeweilige Autor gewählt hat.

Der Umfang der Veröffentlichung ergab sich aus dem Zugeständnis beliebigen Druckraumes an die Plenarvortragenden und von fünf Druckseiten für jeden Symposionsbeitrag. 183 Symposionsbeiträge erforderten dann doch 1100 Seiten. Die Kurzfassungen der Tafelvorträge sind aus Kostengründen unverändert in der während des Kongresses vorgelegten Form und mit den darin enthaltenen Mängeln übernommen. Die Kurzfassungen der Gruppengespräche sind mit unverändertem Text neu gesetzt. Die Titel und die Inhaltsangaben der Filme entsprechen dem Filmprogramm.

Die übersichtliche Anordnung von Beiträgen der verschiedensten Richtungen bedingt Kompromisse. Themenverwandte Symposia sind hintereinandergestellt (siehe auch Seite 176). Ein ausführliches Inhaltsverzeichnis steht hinter diesem Vorwort. Mit einem alphabetischen Verzeichnis aller Autoren (ohne die Titel ihrer Beiträge) und einem Index der wissenschaftlichen Vogelnamen am Schluß des zweiten Bandes habe ich versucht, den Stoff zugänglicher zu machen. Der Übersichtlichkeit nicht dienlich ist die Zerlegung der Verhandlungen in zwei Bände, doch wäre ein Band mit fast 1500 Seiten unhandlich und wenig haltbar gewesen.

Die Manuskripte der Beiträge zu den einzelnen Symposia sind von den jeweiligen Symposionsleitern gelesen und gegebenenfalls bearbeitet worden — so wurde mir jedenfalls versichert. Den größeren Teil der Manuskripte und die betreffenden Korrekturfahnen haben Dr. George A. Clark und Dr. David Snow gelesen, die deutschsprachigen Dr. Dieter Peters. Weitere Korrekturen englischsprachiger Fahnen haben Prof. H.-R. Duncker, Prof. Klaus Immelmann und Dr. Peters vorgenommen. Ihnen allen schulde ich Dank für ihre Hilfe, außerdem Dr. Snow für seine liebenswürdigen und stets wohlbegründeten Ratschläge und meiner Sekretärin, Fräulein Regine Damm, für ihre vielseitige Mitarbeit. Die Umbruchkorrekturen habe ich sämtlich selbst vorgenommen und mich dabei zuweilen gefragt: quis leget haec?

Die Herausgabe der Verhandlungen war nur möglich durch die finanzielle Hilfe der Stiftung Deutsche Klassenlotterie Berlin. Für diese großzügige Förderung einer internationalen Publikation sind wir dem Stiftungsrat und Herrn Direktor Franz Ehrke zu großem Dank verpflichtet.

Ein Wechsel der Druckerei während des Absetzens der Manuskripte, aber auch andere sachliche und persönliche Schwierigkeiten haben das Erscheinen der Verhandlungen über Gebühr verzögert. Soweit ich dafür verantwortlich bin, bitte ich um die Nachsicht der Autoren und Leser.

Berlin, im Oktober 1980

Rolf Nöhring
Generalsekretär



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° Abdusaljamov, Dr. I., Institute of Zoology and Parasitology of Acad. Tadjik Republic, 734025 Duschanbe, General Post-Office, P.O.B. 70, USSR
Able, Dr. K. P., Department of Biology, State University of New York, Albany, New York 12222, USA
Abs, Dr. M., Ruhr-Universität Bochum, Lehrstuhl für Allgemeine Zoologie, Postfach 102148, 4630 Bochum, Bundesrepublik Deutschland
* Abs-Wurmbach, Frau Dr. I.
Adkisson, Dr. C.S., Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, USA
Ahlquist, Dr. J., Peabody Museum, Yale University, New Haven, Conn. 06520, USA
* Ajdukiewicz, Mrs. J., Merton College, Oxford OXI 4JD, United Kingdom
Alden, Dr. P. C., Tour Dir., Natural History Services, Mass. Audubon Society, Lincoln, Mass. 01773, USA
Alerstam, Dr. T., Department of Animal Ecology, 22362 Lund, Sweden
Alleva, Dr. E., Via Belluno 78, 00101 Rome, Italy
Allison, R., 5 Riverside Drive, Mosman Park 6012, Perth, West Australia
Anders, K., Düsseldorfer Str. 4, 1000 Berlin 15, Bundesrepublik Deutschland
Anderson, T. R., Division of Science and Mathematics, McKendree College, Lebanon, Illinois 62254, USA
* Andrade, Mrs. G., chez Dubail, 35 rue de la Tour, 75016 Paris, France
Archibald, Miss N., 30 A Victoria Pk., Toronto M4E 3R9, Ontario, Canada
Arnold, Dr. A. P., Department of Psychology, University of California, Los Angeles, California 90024, USA
Aschoff, Prof. Dr. J., Von der Tannstr. 3, 8131 Andechs, Bundesrepublik Deutschland
Assenmacher, Prof. I., 419 Avenue d'Occitanie, 34100 Montpellier, France
Aubrecht, G., Maria Theresien-Ring 3 A, 2700 WR Neustadt, Österreich
Auzinger, Dr. H., Hirschweg 6 A, 8100 Garmisch-Partenkirchen, Bundesrepublik Deutschland
Aveledo, R., Coleccion Ornitologica Phelps, Apartado 2009, Caracas 101, Venezuela

° Baird, J., Director of Natural History Services, Massachusetts Audubon Society, Lincoln, Mass. 01773, USA
Bairlein, F., Max-Planck-Insitut f. Verhaltensphysiologie, Vogelwarte Radolfzell, Schloß Möggingen, 7760 Radolfzell 16, Bundesrepublik Deutschland
Balát, Dr. F., Uvo Čsav, Květná 8, 60365 Brno, Czechoslovakia,
Balda, R. P., Fakultät für Biologie, Universität Bielefeld, Morgenbreede 45, Postfach 8640, 4800 Bielefeld 1, Bundesrepublik Deutschland
* Balda, Mrs. J. L.
van Balen, Dr. J. H., Institute for Ecological Research, Kemperbergerweg 67, Arnhem, Netherlands
Ball, Dr. I. R., Zoologisch Museum, P.O.B. 20125, 1000 HC Amsterdam, Netherlands
Balthazart, Dr. J., Laboratoire de Biochimie, 17, Place Delcar, 4020 Liège, Belgium
Barlow, Dr. J. C., Department of Ornithology, Royal Ontario Museum, Toronto, Ontario M5S 2C6, Canada
* Barlow, Miss M. B.
Barnard, C., Animal Behaviour Research Group, Department of Zoology, South Parks Road, Oxford 0X1 3PS, United Kingdom
Batten, Dr. L. A., Nature Conservancy Council, 19/20 Belgrave Square, London SW1 X8PY, United Kingdom

Bauer, Dr. K., Direktor, 1. Zool. Abteilung, Naturhistorisches Museum Wien, Postfach 417, 1014 Wien, Österreich
Baumel, Dr. J. J., Department of Anatomy, School of Medicine, Creighton University, Omaha, Nebraska 68178, USA
Baylé, Prof. Dr. J. O., Laboratoire Physiologie Générale, Université Montpellier II — Place E. Bataillon, 34060 Montpellier, France
Bech, C., Department of Zoophysiology, University of Aarhus, 8000 Aarhus C, Denmark
Beck-Peccoz, F. Frhr. von, Ludwigstr. 39, 8890 Aichach, Bundesrepublik Deutschland
Beck, P., Zoologisches Institut, Röntgenring 10, 8700 Würzburg, Bundesrepublik Deutschland
Becker, Dr. P. H., Vogelwarte Radolfzell, Am Obstberg, 7760 Radolfzell 16, Bundesrepublik Deutschland
* Beigel, Frau U., Zoologisches Institut der Universität, Hindenburgplatz 55, 4400 Münster, Bundesrepublik Deutschland
Beintema, Dr. A. J., Research Institute for Nature Management, Kasteel Broekhuizen, Leersum, Netherlands
* Belstler-Glück, Frau I., Beim Kupferhammer 8, 74 Tübingen, Bundesrepublik Deutschland
Belterman, Dr. T., Zoologisch Laboratorium, Plantage Doklaan 44, 1018 CN Amsterdam, Netherlands
Belton, W., C. P. 119, Gramado, RS. 95670, Brazil
* Belton, Mrs. J.
Benson, C. W., Department of Zoology, Downine Street, Cambridge CB2 3EJ, United Kingdom
* Benson, Mrs.
Benvenuti, S., Istituto di Biologia Generale, Via A. Volta 6, 56100 Pisa, Italy
Berger, Dr. M., Westf. Landesmuseum, Himmelreichallee 50, 4400 Münster, Bundesrepublik Deutschland
Berger, R., Hochgasse 55-57, 1180 Wien XVIII, Österreich
* Berger, Frau M.
Bergmann, Dr. H.-H., Fachbereich Biologie-Zoologie, Lahnberge, Postfach 1929, 3550 Marburg, Bundesrepublik Deutschland
Berkhoudt, Dr. H., Zoologisch Laboratorium, Kaiserstraat 63, Leiden, 2300 RA, Netherlands
Berndt, Dr. R., Bauernstr. 13, 3302 Cremlingen 1, Bundesrepublik Deutschland
Berthold, Dr. P., Vogelwarte Radolfzell, Schloß, 7760 Radolfzell 16, Bundesrepublik Deutschland
* Berthold, Frau H.
Bertram, Dr. B., Research Centre, King's College, Cambridge CB2 1ST, United Kingdom
°* Bhargava, A., B4 Officers' Colony, Delhi Road, Saharanpur 247001, India
Biebach, Dr. H., Am Obstberg, 7760 Radolfzell 16, Bundesrepublik Deutschland
Bilcke, G., Department of Biology UIA, Universiteitsplein 1, 2610 Wilryk, Belgium
° Biswas, Dr. B., Zoological Survey of India, Indian Museum, Calcutta 700016, India
Blem, Dr. C. R., Associate Professor, Virginia Commonwealth University, Department of Biology, Academic Div., Richmond Va. 23284, USA
* Blem, Mrs. L. B.
Blondel, J., 24 Chemin de Truchet, 13200 Arles, France
Boag, Prof. D. A., I.T.E. Blackhall, Banchory AB3 3PS, Scotland, United Kingdom
Bock, Prof. W. J., Department of Biological Sciences, Columbia University, New York, N.Y. 10027, USA
Bocxstaele, R. van, Curator of Birds, Koninklijke Maatschappij voor Dierkunde van Antwerpen, Koningin Astridplein 26, 2000 Antwerpen, Belgium
Böhner, J., Mühlenweg 43, 483 Gütersloh 1, Bundesrepublik Deutschland
Boenigk, Dr. G., Niedersächsisches Landesmuseum, Am Maschpark 5, 3000 Hannover 1, Bundesrepublik Deutschland
Boettcher, Frau W., Trabener Str. 43, 1000 Berlin 33, Bundesrepublik Deutschland
° Bogoslowskaja, Dr. L. S., USSR Academy of Sciences, Severtzov Institute of Evolutionary Animal Morphology and Ecology, Moscow, Leninsky prospekt, 33, USSR

de Bont, Prof. Dr. A. F., Walenpotstraat 1 A, 3060 Bertem, Belgium
* de Bont-Hers, Mrs.
Boswall, J., Birdswell, Wraxall, Bristol, BS19 1J2, United Kingdom
Bottjer, P. D., Peabody Museum Nat. Hist., Yale University, New Haven, Conn. 06520, USA
Bourne, A., Academic Press Inc. (London) Ltd., 24-28 Oval Road, London NW1 7DX, United Kingdom
Bourne, Dr. W. R. P., Zoology Department, Tillydrone Ave., Aberdeen, United Kingdom
Bowman, Prof. R. I., Department of Biology, San Francisco State University, San Francisco, Calif. 94132, USA
Bracht, Dr. P., Urfarnstraße 9, 8203 Reisach/Oberaudorf, Bundesrepublik Deutschland
* Bracht, Frau M.
Brauen, A., Ermitage 28, CH-2000 Neuchatel, Schweiz
von Brömssen, A., Zoologiska Institutionen Fack, 400 33 Göteborg 33, Sweden
Bröndum, J., Roarsvej 31, 1 sal, 2000 København V, Denmark
Brown, Dr. R. N., Dept. of Biology, Trent University, Peterborough, Ontario K95 7B8, Canada
Bruderer, Dr. B., Schweiz. Vogelwarte, 6204 Sempach, Schweiz
Brüser, Frl. E., Seelerweg 31, 1000 Berlin 41, Bundesrepublik Deutschland
Bruns, Prof. H., Schloßallee 10a, 6229 Schlangenbad 5, Bundesrepublik Deutschland
Bryant, Dr. D. M., Department of Biology, University of Stirling, Stirling FK9 4LA, Scotland, United Kingdom
Bub, H., Institut für Vogelforschung „Vogelwarte Helgoland", 2940 Wilhelmshaven, Bundesrepublik Deutschland
Bühler, Dr. P., Institut für Zoologie, Universität Hohenheim, 7000 Stuttgart 70, Bundesrepublik Deutschland
° Bull, J., Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, N.Y. 10024, USA
Burton, Dr. P. T. K., British Museum (Natural History), Sub-Department of Ornithology, Park Street, Tring, Herts. HP23 6AP, United Kingdom
Buurma, Dr. L. S., Lisserweg 493, 2165 AS Lisserbroek, Netherlands

Calas, Dr. A., INP08. C.N.R.S., Chemin Joseph-Aiguier 31, 13274, Marseille Cedex 2, France
° Cali, G., 2 Allée du Rouergue, Epernay 51200, France
Carpenter, Dr. F. L., Department Eco. Evol. Biology, University of California, Irvine, Ca. 92717, USA
° Catchpole, Dr. C. K., Bedford College, Regents Park, London NW1 4NS, United Kingdom
Cederholm, G., Tahult 765, 43800 Landuetter, Sweden
° Chandola, Dr. A., Department of Zoology, Banaras Hindu University, Varanasi — 221005, India
Chappuis, C., 24 Rue de Carville, F-76000 Rouen, France
Clark, Dr. R. J., York College of Pennsylvania, Country Club Road, York, Pennsylvania 17405, USA
* Clark, Mrs. J. S.
* Clark, J. P.
Clark, Dr. G. A., Jr., Biological Sciences Group, University of Connecticut, Storrs, CT 06268, USA
* Clifforth, Miss C. J., Roarsvej 31, 1 sal, 2000 København V, Denmark
Cody, Prof. M. L., Department of Biology, University of California, Los Angeles, California 90024, USA
Coles, Dr. R. B., Lehrstuhl für Allgemeine Zoologie, Ruhr-Universität Bochum, 463 Bochum-Querenburg, Bundesrepublik Deutschland
Collette, P., Rue de Jupille 257, 4620 Fleron, Belgium
Collias, Prof. N. E., Department of Biology, University of California, Los Angeles, Cal. 90024, USA

Collins, Dr. C. T., Department of Biology, California State University, Long Beach, California 90840, USA
O'Connor, Dr. R. J., Zoology Department, University College of North Wales, Bangor LL57 2UW, United Kingdom
Conrad, Dr. B., Papenweg 5, 4700 Hamm 1, Bundesrepublik Deutschland
Cooch, Dr. F. G., Canadian Wildlife Service, Ottawa K1A OE7, Canada
Cooke, Dr. F., Department of Biology, Queen's University, Kingston K7L 3N6, Ontario, Canada
Cooper, Dr. R. A., 75 Dobie Ave., Montreal, Quebec H3P 1S1, Canada
* Cooper, E. S.
Coulson, Dr. J. C., Department of Zoology, University of Durham, Durham City, United Kingdom
Cousins, S. H., Technology Faculty, Open University, Milton Keynes, United Kingdom
Cowling, S. J., Fisheries and Wildlife Division, P.O.B. 41, East Melbourne 3002, Australia
* Cowling, Mrs. G. R.
Cracraft, Dr. J., Department of Anatomy, University of Illinois at Medical Center, P.O.B. 6998, Chicago, Illinois 60680, USA
Craig, A., 5 Esserton Flats, 64 College Road, Pietermaritzburg 3201, South Africa
* Craig, Mrs. C.
Cramp, S., 32 Queen's Court, London WC1 N 3BB, United Kingdom
° Creutz, Dr. G., Altes Schloss, 8601 Meschwitz, Deutsche Demokratische Republik
Crombie, P.T., 57 Kitenui Avenue, Mt Albert, Auckland 3, New Zealand
Crowe, T. M., Fitzpatrick Institute, University of Cape Town, P/Bag, Rondebosch 7700, South Africa
* Crowe, Mrs. A.
Croxall, Dr. J. P., British Antarctic Survey, Madingley Road, Cambridge, CB3 OET, United Kingdom
Csicsáky, Dr. M., Zentrum für Anatomie und Cytobiologie, Aulweg 123, 6300 Giessen, Bundesrepublik Deutschland
Curio, Prof. Dr. E., Markstraße 260, 4630 Bochum, Bundesrepublik Deutschland
Curry-Lindahl, Prof. Dr. K., Ministry of Foreign Affairs, Box 16121, 10323 Stockholm 16, Sweden
° Czarnecki, Dr. Z., Zool. Syst. Inst. d. Universität, Fredry 10, 61-701 Poszán, Poland
Czeschlik, Dr. D., Springer Verlag, Neuenheimer Landstraße 28—30, 6900 Heidelberg, Bundesrepublik Deutschland

Dantzler, Prof. W., Department of Physiology, Col. of Med., University of Arizona, Tucson, Arizona 85724, USA
°* Darsono, C. L., P.O.B. 272/kby., Kebayoran, Jakarta Selatan, Indonesia
° Das, S., B-4 Officers' Colony, Delhi Road, Saharanpur 247001, India
°* Das, Dr. M.
°* Das, Mrs. G.
Dathe, Prof. Dr. Dr. H., Am Tierpark 93, 1136 Berlin, Deutsche Demokratische Republik
Dathe, Dr. H. H., Forschungsstelle für Wirbeltierforschung (im Tierpark Berlin), Am Tierpark 125, 1136 Berlin, Deutsche Demokratische Republik
Delacour, J., Amer. Museum-Natural History, Central Park West at 79th St., New York 24, N.Y. 10024, USA
* Demong, Miss N. J., Section of Neurobiology and Behavior, Cornell University, Ithaca, N.Y. 14853, USA
Despin, B., Laboratoire de Thermoregulation, CNRS Faculté de Medicine, 8 av. Rockefeller, 69373 Lyon Cedex 2, France
* Deusser-Schuler, Dr. E., II. Zoolog. Institut und Museum der Universität, Berliner Str. 28, 3400 Göttingen, Bundesrepublik Deutschland
Deutsch, H., MPI f. Physiol. u. Klin. Forschung, W. G. Kerckhoff-Institut, 6350 Bad Nauheim, Bundesrepublik Deutschland
Deviche, P., Laboratoire de Biochimie, Gen. et Comp., Place Delcour 17, 4020 Liège, Belgium

Devillers, Dr. P., Institut royal des sciences naturelles, rue Vautier 31, 1040 Bruxelles, Belgium
Diamond, Dr. J. M., University of California, School of Medicine, Physiology Department, Los Angeles, CA 90024, USA
Dittami, J., Max Planck Institut, 8131 Andechs, Bundesrepublik Deutschland
* Dixor, Mrs. J. D., Colección Ornitologica Phelps, Apartado 2009, Caracas 101, Venezuela
* Dohmann, Frau M., Wahlhau 19, 74 Tübingen 7, Bundesrepublik Deutschland
Dorka, Dr. V., Zool. Institut der Universität, Biologie III, Auf der Morgenstelle 28, 74 Tübingen, Bundesrepublik Deutschland
Dornberger, W., Rathausgasse 8, 6994 Niederstetten, Bundesrepublik Deutschland
Dornfeldt, Dr. K., 1. Zoologisches Institut, Berliner Str. 28, 3400 Göttingen, Bundesrepublik Deutschland
° Dorst, Prof. J., Museum, 57 rueCuvier, 75231 Paris Cedex 05, France
Dow, Dr. D. D., Department of Zoology, University of Queensland, St. Lucia, QLD., 4067, Australia
Dowsett, R.J., Nyiko National Park, Private Bog Chilinda, PO Rumphi, Malawi
Drent, Dr. R. H., Zoölogisch Lab., Kerklaan 30, Haren (Gron) Netherlands
von Düring, Dr. M., Anatomisches Institut II, Universitätsstr. 150, MA, 6. O.G., 4630 Bochum 1, Bundesrepublik Deutschland
Duncker, Prof. Dr. Dr. H.-R., Zentrum für Anatomie und Cytobiologie der Justus Liebig-Universität, 6300 Gießen, Aulweg 123, Bundesrepublik Deutschland
* Dutton, Miss D. A., c/o Department of Biology, University of California, Los Angeles, California 90024, USA
Duval, F., Argentinische Allee 3, 1000 Berlin 37, Bundesrepublik Deutschland
Dyck, J., Institute of Comparative Anatomy, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark
Dyer, Dr. M. I., Professor, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, USA
Dyrcz, Dr. A., Zoological Institute Wrocław University, Sienkiewicza 21, 50-335 Wrocław, Poland
Dzerzhinski, F. Y., Faculty of Biology Moscow, Lomonosow State University, 117234 Moscow, USSR

Ebenhöh, Dr. H., Wiesenstr. 32, 7830 Emmendingen, Bundesrepublik Deutschland
* Ebenhöh, Frau G.
Ehrhardt, D., Berliner Str. 80, 1 Berlin 37, Bundesrepublik Deutschland
Eisenmann, Dr. E., American Museum of Natural History, 79th Street and Central Park West, New York, N.Y. 10024, USA
Ekman, J., University of Gothenburg, Department of Zoology, Fack. 40033 Gothenburg 33, Sweden
Elliott, Sir H., 173 Woodstock Road, Oxford 0X2 7NB, United Kingdom
Elliott, Dr. C., Fao Project Quelea, P.O.B. 21, N'Djamena, Tchad
° Ellis, B. A., 44 Braithwaite Street, Wellington 5, New Zealand
°* Ellis, Mrs. B. A.
Elvers, J.-H., Fischerhüttenstr. 40, 1000 Berlin 37, Bundesrepublik Deutschland
* Elzer, Mrs. E., 4689 Westmount Avenue, Westmount, Quebec H3Y 1X2, Canada
Emlen, Dr. S. T., Professor of Animal Behavior, Section of Neurobiology and Behavior, Cornell University, Ithaca, N.Y. 14853, USA
Engel, A., Alpenblickstr. 15, 7827 Löffingen-Göschweiler, Bundesrepublik Deutschland
Engel, E., Otawistraße 21, 1000 Berlin 65, Bundesrepublik Deutschland
Erard, C., Zoologie (Mammiféres et Oiseaux), 55 rue de Buffon, 75005 Paris, France
Erdelen, M., Zoologisches Institut der Universität Köln, I. Lehrstuhl, Weyertal 119, 5000 Köln 41, Bundesrepublik Deutschland
* Erdelen, Frau B.
° Erickson, Dr. M. M., Department of Biological Sciences, University of California, Santa Barbara, California 93106, USA

Erskine, Dr. A. J., P.O.B. 1327 Sackville, N.B., E0A 3C0, Canada
Escher-Gräub, D., Obere Bachgasse 8, 84 Regensburg, Bundesrepublik Deutschland
Esser, P., Menglinghauserstr. 35, 4600 Dortmund 50, Bundesrepublik Deutschland
Ewald, P., Department of Zoology, NJ-15, University of Washington, Seattle WA. 98198, USA

Faaborg, Dr. J., 106 Tucker Hall, University of Missouri-Columbia, Columbia, Missouri 65201, USA
Fabricius, Prof. E., Zoologiska Inst., Stockholms Univ., Box 6801, 113 86 Stockholm, Sweden
* Fabricius, Mrs. H.
Falls, Dr. J. B., Department of Zoology, University of Toronto, Toronto, Canada M5S IAI
Farner, Prof. D. S., Department of Zoology, University of Washington, Seattle, WA 98195, USA
* Farner, Mrs. D. C.
Faust, Frau Dr. I., Pfarrer-Hebererstr. 46, 653 Bingen, Bundesrepublik Deutschland
Feare, Dr. C. J., Pest Infestation Contral. Lab., Trangley Place, Worplesdon, Surrey, United Kingdom
Fedde, Dr. M. R., Department Anatomy and Physiology, Kansas State University, Manhattan, Kansas 66506, USA
Feduccia, Dr. J. A., Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27514, USA
* Feduccia, Mrs. O. T.
* Fergenbauer, Frau A., Universität Frankfurt, Siesmayerstr. 70, 6000 Frankfurt, Bundesrepublik Deutschland
Ferry, Dr. C., Faculté de Medecine, 21000 Dijon, France
Finn, Miss N. E., 78 B St. Andrews Hill Road, Christchurch 8, New Zealand
Fischer-Nagel, A., Dipl. Biol., Ahrenshooper Zeile 63, 1000 Berlin 38, Bundesrepublik Deutschland
* Fischer-Nagel, Frau H.
Fitzpatrick, Dr. J. W., Bird Division, Field Museum of Natural History, Roosevelt Rd. at Lake Shore Drive, Chicago, Illinois 60605, USA
Fiuczynski, Dr. D., Klingsorstr. 27, 1000 Berlin 41, Bundesrepublik Deutschland
Follett, Prof. B. K., Department of Zoology, University College, Bangor, N. Wales, United Kingdom
Forbes-Watson, Dr. A. D., Animal Ecology Research Group, Zoology Dept., Oxford University, South Parks Road, Oxford, United Kingdom
Forshaw, J. M., Australian National Parks and Wildlife Service, P.O.B. 636, Canberra City, ACT 2601, Australia
Franke, Frau E., Große Köhlergasse 1, 6360 Friedberg 1, Bundesrepublik Deutschland
Frädrich, Dr. H., Budapester Str. 32, 1000 Berlin 30, Bundesrepublik Deutschland
* Frädrich, Frau Dr. J.
Frith, Dr. H. J., Csiro Wildlife Division, P.O.B. 84, Lyneham, 2602, Australia
* Frith, Mrs. D. M.
Fritsche, Frau G., Institut für Verhaltensphysiologie, Universität Bielefeld, Postfach 8640, 4800 Bielefeld, Bundesrepublik Deutschland
Fritz, R. S., Department of Zoology, University of Maryland, College Park, Maryland 20742, USA
Frochot, Prof. B., Laboratoire d'Ecologie, Université de Dijon, 21000 Dijon, France
Frost, P.G.H., P.O.B. 106, 3867 Mtunzini, Natal, South Africa
* Frost, Mrs. S. K.
Frugis, Prof. S., Director of Italian Center of Ornithological Studies, Zool. Institute, Parma, Italy
* Frugis, Mr.
Fry, Dr. C. H., Aberdeen University Zoology Department, Tillydrone Avenue, Aberdeen AB9 2TN, Scotland, United Kingdom

* Fry, Mrs. K.
Fuchs, Dr. E., Leiter der Schweiz. Vogelwarte, 6204 Sempach, Schweiz
Furrer, Dr. R. K., Schweiz. Vogelwarte, 6204 Sempach, Schweiz

Gänshirt, Frau G., Max Planck-Institut, 8131 Erling-Andechs, Bundesrepublik Deutschland
° Galushin, Dr. V. M., Zoology Department, Moscow State Pedagogical Institute, Kibalchicha 6, Moscow, I-243, USSR
Garson, P. J., Department of Zoology, University of Newcastle upon Tyne, Newcastle upon Tyne, NE1 7RU, United Kingdom
Gaston, Dr. A. J., Edward Grey Institute, Department of Zoology, South Parks Road, Oxford, United Kingdom
Gatter, W., Forsthaus, 7318 Lenningen-Schopfloch, Bundesrepublik Deutschland
Gauthreaux, Jr., Dr. S. A., Department of Zoology, Clemson University, Clemson, SC 29631, USA
* McGeer-Redpath, Mrs., Hahn-Meitner-Institut für Kernforschung, Glienicker Str. 100, 1000 Berlin 37, Bundesrepublik Deutschland
Gehlbach, Prof. F. R., Department of Biology, Baylor University, Waco, TX 76703, USA
* Gehlbach, Mrs. N. Y.,
° Geinitz, C., Institut für Biologie I (Zoologie), Albertstraße 21 A, 7800 Freiburg, Bundesrepublik Deutschland
Géroudet, Dr. P., 37 Av. de Champel, 1206 Genève, Schweiz
* Géroudet, Mrs. C.
Gibbs, Dr. M., School of Biology, the University of Sussex, Brighton, BN1 9QG, United Kingdom
Gill, Dr. F. B., Academy of Natural Sciences, 19th St. and Parkway, Philadelphia, PA. 19103, USA
Glück, E., Beim Kupferhammer 8, 7400 Tübingen, Bundesrepublik Deutschland
Glutz von Blotzheim, Prof. Dr. U., „Eichhölzli", Mattweid 20, 6240 Sempach, Schweiz
* Glutz von Blotzheim, Frau A. M.
Goethe, Dr. F., Kirchreihe 19 B, 2940 Wilhelmshaven, Bundesrepublik Deutschland
* Goethe, Frau E.
Goldstein, H., 3/224 Longueville Rd., Lane Ceve 2066, Australia
* Goldstein, Mrs. B.
Gonzalez, D. J. A., Morales, Ruamayor 4, Santander, Spain
Gove, C. N., 6 Henley Street, Balwyn Victoria 3103, Australia
* Gove, Mrs. J.
° Graczyk, Prof. Dr. R., Institute of Applied Zoology, Agricultural Academy, u. Wojska Polskiego 71 C, 60-625 Poznan, Poland
Graf, R., Inst. Tierphysiologie, Ruhr-Universität Bochum, Universitätsstr. 150, 4630 Bochum, Bundesrepublik Deutschland
Greenwell, G. A., Smithsonian Institution, National Zoological Park, Washington, D.C. 20009, USA
Grillet, L., Docteur Vétérinaire, 85620 Rocheservière, France
Grosskopf, G., Asternweg 7, 2160 Stade-Schölisch, Bundesrepublik Deutschland
Grüter, G., Weberstr. 25, 6000 Frankfurt 1, Bundesrepublik Deutschland
Güntert, M., Zoologisches Museum der Universität, Künstlergasse 16, 8006 Zürich, Schweiz
Güttinger, H. R., FB Biologie der Universität, 675 Kaiserslautern, Bundesrepublik Deutschland
Guillet, Dr. A., Percy Fitzpatrick Institute of African Ornithology, Rondebosch 7700, South Africa
Gulledge, J. L., Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, N. Y. 14853, USA
Gunn, Dr. W. W. H., P.O.Box 1229, Spruce Grove, Alberta TOE 2C0, Canada
Gwinner, Dr. E., Max-Planck-Institut für Verhaltensphysiologie, 8131 Erling-Andechs, Bundesrepublik Deutschland
* Gwinner, Frau H.

Haartman, Freiherr von, Prof. Dr. L., Department of Zoology, University of Helsinki, P. Rautatieck. 13, SF-00100 Helsinki 10, Finland

* Haartman, Freifrau von, B.

Haas, V., Spezialberatung für Pflanzenschutz, Gartenstr. 2, 7770 Überlingen a. B., Bundesrepublik Deutschland

Haase, Prof. Dr. E., Institut für Haustierkunde, Neue Universität, 2300 Kiel, Bundesrepublik Deutschland

Haffer, Dr. J., Tommesweg 60, 4300 Essen 1, Bundesrepublik Deutschland

Hainsworth, Dr. F. R., Department of Biology, Syracuse University, Syracuse, N.Y. 13210, USA

Haller, H., Museumstr. 13, 7260 Davos, Schweiz

* Hallmann, Frau, Fernkorngasse 43/1, 1100 Wien X, Österreich

Hammel, Prof. H. T., A-004, Scripps Institution of Oceanography, La Jolla, CA 92093, USA

Hand, Mrs. J. L., Biology Department, University of California, Los Angeles, California, USA

Hartmann, Frau B., Kaiser-Friedrich-Ring 69, 6200 Wiesbaden, Bundesrepublik Deutschland

Hartmann-Müller, Frau B., Am Roßgang 3, 3504 Kaufungen 1, Bundesrepublik Deutschland

Hartner, Dr. L., Universität Hohenheim, Institut für Zoophysiologie, Garbenstr. 30, 7000 Stuttgart 70, Bundesrepublik Deutschland

Hartwig, Dr. H.-G., Zentrum für Anatomie und Cytobiologie, Aulweg 123, 6300 Giessen, Bundesrepublik Deutschland

Hauschildt, Dr. E., Kreuzfurth 12, 2000 Hamburg 62, Bundesrepublik Deutschland

* Hauschildt, Frau I.

Heike, D., Monumentenstr. 36, 1000 Berlin 62, Bundesrepublik Deutschland

Heinrich, Dr. W., I. Zoologisches Institut, Berliner Straße 28, 3400 Göttingen, Bundesrepublik Deutschland

Heinroth, Dr. K., Händel-Allee 7, 1000 Berlin 21, Bundesrepublik Deutschland

Helb, Dr. H. W., Fachbereich Biologie der Universität, Postfach 3049, 6750 Kaiserslautern, Bundesrepublik Deutschland

von Helversen, Dr. D., Biologisches Institut I (Zoologie) der Universität, Albertstr. 21, 7800 Freiburg, Bundesrepublik Deutschland

Herrera, Dr. C. M., Virgen de la Presentación 2, Sevilla 1, Spain

Heuwinkel, H., Zoologisches Institut der Universität, Hindenburgplatz 55, 4400 Münster, Bundesrepublik Deutschland

Hölzinger, Dr. J., Am Obstberg, 7760 Radolfzell 16, Bundesrepublik Deutschland

Hoffmann, Dr. L., Tour du Valat, 13200 Le Sambuc, France

Hofstetter, F. B., Königsberger Allee 26, 2210 Itzehoe, Bundesrepublik Deutschland

* Hofstetter, Frau D.

Holgersen, Dr. H., Stavanger Museum, 4000 Stavanger, Norway

* Holgersen, Mrs. B.

Holmes, Dr. R. T., Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755, USA

Holyoak, D. T., Geography Department, University of Reading 2, Earley Gate, Whiteknights Road, Reading RG6 2AU, United Kingdom

Homberger, Dr. D. G., Department of Biological Sciences, Columbia University, New York, N.Y. 10027, USA

* Horne, Mrs. J. F. M., Ornithology, American Museum of Nat. History, 79 St. and Central Park West, New York, N.Y. 10024, USA

° Horváth, Dr. L., Hungarian Natural History Museum, 1088 Budapest, Baross u. 13, Hungary

Houston, Dr. D. C., Zoology Department, Glasgow University, Glasgow G12 8QQ, United Kingdom

Howell, T. R., Department of Biology, University of California, Los Angeles, CA 90024, USA

Hudec, Dr. K., ČSAV, Institute of Vert. Zoology, 60365 Brno, Kvetná 8, Czechoslovakia

Hulsman, Dr. K., c/o Dr. S. Daan, Skyligerwei 4, 9135 PH Morra (Fr.), Netherlands

Hultsch, Frl. H., Muthesiusstr. 38, 1000 Berlin 41, Bundesrepublik Deutschland
Hummel, Prof. Dr. D., Institut für Strömungsmechanik, TU Braunschweig, Bienroder Weg 3, 3300 Braunschweig, Bundesrepublik Deutschland
Hunter, M. L., Edward Grey Institute, Department of Zoology, Oxford, United Kingdom
° Hunter, Dr. M., P.O.Box 311, Albury NSW, Australia 2640

Ilyichev, Prof. Dr. V., Institute of Evolutionary Morphology and Ecology of Animals, USSR Academy of Sciences, Moscow, Leninski Prospekt 33, USSR
Immelmann, Prof. Dr. K., Fakultät für Biologie, Postfach 8640, 4800 Bielefeld 1, Bundesrepublik Deutschland
* Immelmann, Frau G.
Ingels, Dr. J., Galgenberglaan 9, 9120 Destelbergen, Belgium
° Isakov, Prof. Dr. Y., 109017, Institute of Geography, USSR Academy of Sciences, Staromonetny 29, Moscow, USSR

Jacob, Dr. J., Biochem. Inst. f. Umweltcarcinogene, Sieker Landstr. 19, 2070 Ahrensburg, Bundesrepublik Deutschland
° Jacoby, Dr. V., Inst. Evol. Animal Morph. and Ecology, Leninski Prospekt 33, A. N. Severtzov, 117071 Moscow, USSR
Jänicke, B., Regensburger Str. 39, 1000 Berlin 30, Bundesrepublik Deutschland
Järvinen, O., Department of Genetics, University of Helsinki, P. Rautatiekatu 13, Helsinki 10, Finland
d'Jamous, R., c/o I.W.P.F., Section France, 52 av. Duquesne, Paris, France
Jansson, C., Zoologiska Institutionen Fack, 40033 Göteborg 33, Sweden
Jarry, G., Société Ornithologique de France, 55 rue Buffon, 75005 Paris, France
Jellis, Miss R. E., Woodway, Pinner Hill, Pinner, Middx. HA5 3XU, United Kingdom
° Johansen, Prof. K., Department of Zoophysiology, University of Aarhus, 8000 Aarhus C., Denmark
Johnsgard, Prof. P. A., School of Life Sciences, University of Nebraska-Lincoln, Lincoln, Nebraska 68588, USA
Johnson, A. R., Station Biologique, La Tour du Valat, Le Sambuc, 13200 Arles, France
Johnstone, Dr. G. W., Antarctic Division, 568 St. Kilda Road, Melbourne, 3004, Australia
Joiris, Dr. C., Laboratorium Ekologie en Systm., Vrije Universiteit Brussel, Pleinlaan 2, 1050 Brussel, Belgium
Jouanin, Dr. C., 42 rue Charles Laffitte, 92200 Neuilly sur Seine, France
°* Jouanin, Mme C.

° Kaiser, H., Kierlingerstraße 75, 3400 Klosterneuburg, Österreich
Kalabér, L., 4225 Reghin, Eminescu 26, Rumania
* Kalabér, Mme R. M.
Kalchreuter, Dr. H., Arbeitsstelle für Wildforschung, 7823 Bonndorf-Glashütte, Bundesrepublik Deutschland
Kalisch, H.-J., Böcklinstr. 53, 318 Wolfsburg, Bundesrepublik Deutschland
Karcher, M., Hirtenstr. 31, 8057 Eching, Bundesrepublik Deutschland
* Karcher, Frau H.
Karlsson, J., Department of Animal Ecology, Ecology Building, Helgonavägen 5, 223 62 Lund, Sweden
Karr, Dr. J. R., Department of Ecology, Ethology and Evolution, ıVivarium Building, University of Illinois, Champaign, Illinois 61820, USA
Kasche, C., Haus 11 A, 3133 Leisten, Post Schnega, Bundesrepublik Deutschland
° Kasparek, M., Bettinaweg 7, 8300 Landshut, Bundesrepublik Deutschland
°* Kaur, Miss G., B-4 Officers' Colony, Delhi Road, Saharanpur 247001, India
Kear, Dr. J., The Wildfowl Trust, Martin Mere, Burscough, Nr. Ormskirk, Lancs., United Kingdom
Keast, Prof. A., Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

KEETON, Prof. W. T., Liberty Hyde Bailey, Prof. of Biology, Section of Neurobiology and Behavior, 143 Langmuir Laboratory, Cornell University, Ithaca, New York 14850, USA

KELSALL, Dr. J. P., 22 Deerfield Drive, Delta, British Columbia V4M 2W9, Canada

* KELSALL, Mrs. J. I.

°* KELSALL, Miss P. J.

KETTLE, R., British Institute of Recorded Sound, 29 Exhibition Road, London SW7 2AS, United Kingdom

KIEPENHEUER, Dr. J., Abt. für Verhaltensphysiologie, Beim Kupferhammer 8, 7400 Tübingen, Bundesrepublik Deutschland

KIFF, L. F., Curator, Western Foundation of Vertebrate Zoology, 1100 Glendon Ave., Los Angeles, CA 90024, USA

* KIFF, Mrs. J. L.

KIKKAWA, Dr. J., c/o Edward Grey Institute, Department of Zoology, South Parks Road, Oxford OXI 3PS, United Kingdom

KING, Dr. J. R., Department of Zoology, Washington State University, Pullman, Washington 99164, USA

* KING, Miss J. M.

KING, W. B., 871 Dolley Madison Blvd., McLean, VA 22101, USA

KLEIN, Dr. H., Max-Planck-Institut für Verhaltensphysiologie, Hörndlweg 14, 8131 Andechs, Bundesrepublik Deutschland

KLÖS, Prof. Dr. H.-G., Budapester Str. 32, 1000 Berlin 30, Bundesrepublik Deutschland

* KLÖS, Frau U.

KNOX, Dr. A., Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB9 2TN, Scotland, United Kingdom

KNUDSEN, Dr. E. I., 2034 Glenview, Altadena, CA 91001, USA

KOBAYASHI, Prof. H., Misaki Marine Biological Station, University of Tokyo, Misaki, Miurashi, Kanagawa-Ken, 238-02, Japan

KÖNIG, Dr. C., Staatliches Museum für Naturkunde, Schloß Rosenstein, 7000 Stuttgart 1, Bundesrepublik Deutschland

KOKSHAYSKY, Dr. N. V., Severtzov Institute of Evolutionary Animal Morphology and Ecology, USSR Academy of Sciences, Leninsky Prospekt 33, Moscow W-71, USSR

KORTSTOCK, K., Institut für Verhaltensphysiologie, Universität Bielfeld, Postfach 8640, 4800 Bielefeld 1, Bundesrepublik Deutschland

KOWALSKI, H., Centre d'Ecologie de Camargue, Le Sambuc, 13200 Arles, France

KREBS, Dr. J. R., Edward Grey Institute of Field Ornithology, South Parks Road, Oxford OXI 3 PS, United Kingdom

KREITHEN, Dr. M. L., Research Associate Lecturer, Section of Neurobiology and Behavior, 154 Langmuir Laboratory, Cornell University, Ithaca, N.Y. 14850, USA

KUHK, Dr. R., Schloß Möggingen, 7760 Radolfzell 16, Bundesrepublik Deutschland

KUMERLOEVE, Dr. H., Hubert-Reissner-Str. 7, 8032 Gräfelfing, Bundesrepublik Deutschland

* KUMERLOEVE, Frau G.

° KUROCHKIN, E. N., Paleontological Museum of the USSR Academy of Sciences, Leninsky Prospekt 16, Moscow 117071, USSR

LAMMERS, F., Mozartweg 11, 4837 Verl 1, Bundesrepublik Deutschland

LAMMERS, Dr. R., Kettelerstr. 5, 4837 Verl 1, Bundesrepublik Deutschland

LANDOLT, Frau R., Schachenstr. 6, 8907 Wettswil, Schweiz

LANDSBERG, J.-W., Knesebeckstr. 2, 1000 Berlin 45, Bundesrepublik Deutschland

LANE, J. A. K., W. A. Wildlife Research Centre, P.O.B. 51, Wanneroo, Western Australia

LEDERER, Dr. R. J., Department of Biological Sciences, California State University, Chico, CA, USA

LEES-SMITH, D. T., 134 The Avenue, Starbeck, Harrogate, North Yorkshire HG1 4QF, United Kingdom

LEISLER, Dr. B., Vogelwarte Radolfzell, Am Obstberg, 7760 Radolfzell, Bundesrepublik Deutschland

LEMAIRE, Mlle F., Rue de Bois de Breux 194, 4500 Jupille, Belgium
LENNON, Mrs. E. S., 5179 Oasis Road, Redding, CA 96001, USA
LEPPELSACK, Dr. H.-J., Lehrstuhl für Allgemeine Zoologie, Ruhr-Universität Bochum, 463 Bochum-Querenburg, Bundesrepublik Deutschland
LÉVÊQUE, R., Schweizerische Vogelwarte, 6204 Sempach, Schweiz
LIGON, Dr. J. D., Department of Biology, The University of New Mexico, Albuquerque, N.M. 87191, USA
* LIGON, Mrs. S. H.
° LING, Mrs. Assist.-Prof. R., 202400 Tartu, Mitchurini 19-4, Estonian SSR, USSR
LIVERSIDGE, Dr. R., McGregor Museum, Box 316, Kimberley 8300, South Africa
LÖHRL, Dr. H., Edelweiler 73, 7293 Pfalzgrafenweiler 2, Bundesrepublik Deutschland
LÖPPENTHIN, B., Torvevej 14, 2740 Skovlunde, Denmark
* LÖPPENTHIN, Mrs. G.
LOETZKE, W.-D., Eislebener Str. 6, c/o Wagner, 1000 Berlin 30, Bundesrepublik Deutschland
LOMHOLT, Dr. J. P., Department of Zoophysiology, University of Aarhus, 8000 Aarhus C., Denmark
LORENZ, Prof. Dr. K., Österreichische Akademie der Wissenschaften, Institut für Vergl. Verhaltensforschung, Adolf-Lorenz-Gasse 2, 3422 Altenberg, Österreich
LOUETTE, Dr. M., Koninklijk Museum voor Midden-Afrika, 1980 Tervuren, Belgium
LOVEJOY, T., World Wildlife Fund, 1601 Connecticut Ave. N. W. F., Washington, D.C. 20009, USA
LUNIAK, Dr. M., Institute of Zoology, Wilcza 64, P.O.B. 1007, 00-950 Warszawa, Poland
LYSTER, I. H. J., Royal Scottish Museum, Edinburgh EH1 1JF, Scotland, United Kingdom

MACHE, R., Moenchstraße 3, 7000 Stuttgart 1, Bundesrepublik Deutschland
MAHER, Dr. W. J., Bangor Research Station, Penrhos Road, Bangor Gwynedd, United Kingdom
LE MAHO, Dr. Y., Laboratoire de Thermoregulation, CNRS Faculté de Medicine, 8 av. Rokkefeller, 69373 Lyon Cedex 2, France
MAKATSCH, Dr. W., Martin-Hoop-Straße 43, 86 Bautzen 1, Deutsche Demokratische Republik
* MAKATSCH, Frau I.
° MALMBERG, Dr. T., Plommonvägen 1, 22355 Lund, Sweden
MANIKOWSKI, S., Laboratory of Animal Ethology, Jaqiellonian University, Krupnicza 50, 30-060 Krakow, Poland
MANLEY, Prof. Dr. G., c/o Lehrstuhl für Elektroakustik der Technischen Universität München, Arcisstr. 21, 8000 München 2, Bundesrepublik Deutschland
MARLER, P., Professor and Director, Rockefeller University Field Research Center, Tyrrel Road, Millbrook, N.Y. 12545, USA
MARTIN, Dr. L. D., Museum of Natural History, University of Kansas, Lawrence, Kansas 66045, USA
MATTES, H., Institut für Ökologie, Albrecht-Thaer-Weg 4, 1000 Berlin 33, Bundesrepublik Deutschland
MATVEJEV, Dr. S., ul. Milčinskega 14, 6100 Ljubljana, Yugoslavia
MAXSE, Miss V., Hatchett Westburton, Pulborough, Sussex RH20 IHD, United Kingdom
MAYR, Prof. E., 11 Chauncy Str., Cambridge, Ma. 02138, USA
* MAYR, Mrs. G.
MEBES, H.-D., Fachbereich Biologie der Universität, Postfach 3049, 6750 Kaiserslautern, Bundesrepublik Deutschland
MEES, G. F., Rijksmuseum van Natuurlijke Historie, P.O.B. 9517, 2300 RA Leiden, Netherlands
MEIER, Prof. A. H., Department of Zoology, Louisiana State University, Baton Rouge, Louisiana 70803, USA
* MEIER, Mrs. A. M.
MEISE, Prof. Dr. W., Am Weiher 23, 2000 Hamburg 19, Bundesrepublik Deutschland
* MEISE, Frau E.

Menaker, M., Department of Zoology, University of Texas at Austin, Austin, Texas, USA
Mendelssohn, Prof. H., Department of Zoology, Tel Aviv University, 155 Herzl St., Tel Aviv, Israel
* Mendelssohn, Mrs. T.
Merkel, Prof. F. W., Karlsbader Str. 19, 6370 Oberursel/Ts., Bundesrepublik Deutschland
* Merkel, Frau I.
Merne, O. J., Forest and Wildlife Service, Sidmonton Pl., Bray, Co. Wicklow, Ireland
Mertens, Dr. J. A. L., c/o Institute for Ecological Research, Kemperbergerweg 67, Arnhem, Netherlands
Metzmacher, Dr. L., Rimpaustr. 8, 3000 Hannover 1, Bundesrepublik Deutschland
Meyburg, B.-U., Herbertstr. 14, 1000 Berlin 33, Bundesrepublik Deutschland
* Meyburg, Frau C.
Middleton, Dr. A. L. A., Department of Zoology, University of Guelph, Guelph, Ontario NIG 2WI, Canada
Miller, Dr. D. B., Box 7595, Dorothea Dix Hospital, Raleigh, North Carolina 27611, USA
* Miller, Mrs. L. L.
Mocci Demartis, Dr. A., c/o Istituto di Zoologica (Univ.) Viale Poetto 1, 09100 Cagliari, Italy
Møller, H. S., Skovfogedhuset, Snaptun, 8700 Horsens, Denmark
Möller, Prof. Dr. W., Zentrum für Anatomie und Cytobiologie, Aulweg 123, 6300 Gießen, Bundesrepublik Deutschland
* Möller, Frau G.
Monaghan, Dr. P., Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Scotland, United Kingdom
Montgomery, G. H., 4689 Westmount Avenue, Westmount, Quebec H3Y 1X2, Canada
* Montgomery, Mrs. M.
Morel, Dr. G. J., O.R.S.T.O.M., Station d'Ecologie, P.O.B. 20, Richard Toll, Senegal
* Morel, Mme J. Y.
Morgan, P. J., B.Sc., M.I.Biol., A.M.A., M.B.O.U., Keeper of Vertebrate Zoology, Merseyside County Museums, William Brown Street, Liverpool L3 8EN, United Kingdom
Moritz, Dr. D., Postfach 1220, 2192 Helgoland, Bundesrepublik Deutschland
Morlion, Dr. M., Houthulststraat 13, 8000 Brugge, Belgium
Morton, Dr. E. S., National Zoological Park, Smithsonian Institution, Washington, D.C. 20008, USA
Mougin, Dr. J.-L., Museum National d'Histoire Naturelle, 55 Rue de Buffon, 75000 Paris 5 e, France
Müller, W., Kleinalbis 74, 8045 Zürich, Schweiz
Mueller, H. C., Department Zoology, Univ. N.C., Chapel Hill, N.C. 27514, USA
* Mueller, Mrs. N. S.
Munn, C. A., Merton College, Oxford OXI 4JD, United Kingdom
Murphy, E. C., Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99701, USA
Murphy, Dr. J. R., Department of Zoology, 167 WIDB, Brigham Young University, Provo, Utah 84602, USA
* Myers, Miss D. J., York College of Pennsylvania, Country Club Road, York, Pennsylvania 17405, USA

McNabb, Dr. R. A., Biology Department, Va. Polytech. Inst. and State University, Blacksburg VA 24061, USA
* McNabb, Dr. F. M. A.
Nachtigall, Prof. W., Zoologisches Institut der Universität, 6600 Saarbrücken, Bundesrepublik Deutschland
Nakamura, Prof. T., Department of Biology, Yamanashi University, Kofu 400, Japan
° Navasaitis, Dr. A., Kaunas Akademija, LŽUA, Miškininkystės kat., Lithuania 233000, USSR
* Nebelsiek, Dr. U., Münchhausenweg 11, 2 Hamburg 61, Bundesrepublik Deutschland
Necker, Dr. R., Institut für Tierphysiologie, Postfach 102148, 4630 Bochum 1, Bundesrepublik Deutschland

Nehls, Dr. H. W., Zoologischer Garten Rostock, Tiergartenallee 10, 25 Rostock, Deutsche Demokratische Republik
Newton, Dr. I., 12 Hope Terrace, Edinburgh EH9 2AS, Scotland, United Kingdom
Nicholson, Dr. E. M., 13 Upper Cheyne Row, London SW3 5JW, United Kingdom
Nicolai, Dr. J., Institut für Vogelforschung „Vogelwarte Helgoland", 2940 Wilhelmshaven-Rüstersiel, Bundesrepublik Deutschland
* Nicolai, Frau A.
Nieboer, Dr. E., Biological Laboratories, Free University, De Boele Laan 1087, Amsterdam, Netherlands
Nöhring, R., Zoologischer Garten, Hardenbergplatz 8, 1000 Berlin 30, Bundesrepublik Deutschland
* Nöhring, Frau I.
Nolan Jr., V., Department of Biology, Indiana University, Bloomington, Indiana 47401, USA
Nolte, Frau B., Falkengrund 11, 2085 Quickborn, Bundesrepublik Deutschland
North, Dr. C. A., Department of Biology, UW-W, Whitewater, Wis. 53190, USA
Nottebohm, Dr. F., Field Research Center, Rockefeller University, Millbrook, N.Y. 12545, USA
Nowak, Dr. E., Institut für Naturschutz und Tierökologie (BFANL), Konstantinstr. 110, 5300 Bonn 2, Bundesrepublik Deutschland
° Novikov, Prof. B. G., Kiev State University, Faculty of Biology, Vladmirskaya 60, 25017 Kiev-17, USSR

° Oeckinghaus, H., Hünxerstr. 347, 4220 Dinslaken, Bundesrepublik Deutschland
Öhman, Mr. C. G., P.O.B. 98, 56023 Bankeryd, Sweden
* Öhman, Mrs. E.
Oehme, Dr. H., Akademie der Wissenschaften der DDR, Forschungsstelle für Wirbeltierforschung (im Tierpark Berlin), Am Tierpark 125, 1136 Berlin, Deutsche Demokratische Republik
Oelke, Prof. Dr. H., Kastanienallee 13, 315 Peine, Bundesrepublik Deutschland
° Oesman, Dr. H. M. K., P.O.B. 272/Kby., Kebayoran, Jakarta Selatan, Indonesia
°* Oesman, Mrs. K.
Österlöf, S., Bird-Ringing Office, Swedish Museum of Natural History, 10405 Stockholm, Sweden
Ogasawara, Dr. K., Department of Biology Education, Akita University, 010 Tegata Akita, Japan
Ogden, J. C., National Audubon Research, 115 Indian Mound Trail. Tavernier, Florida 33070, USA
* Ogden, Mrs. M. B.
Ohm, Prof. Dr. D., Technische Universität Berlin, Lehrgebiet f. Zoologie, Holbeinstraße 5, 1000 Berlin 45, Bundesrepublik Deutschland
°* Ohm, Dr. I.-D.
° Ojanen, M., Oulu University, LTK/Biology, Kajaanintie 52 A, 90220 Oulu 22, Finland
Oka, Miss N., c/o Yamashina Institute for Ornithology, 8-20 Nampeidai-machi, Shibuja-ku, Tokyo, 150 Japan
Oksche, Prof. Dr. A., Zentrum für Anatomie und Cytobiologie, Justus Liebig-Universität, Aulweg 123, 6300 Gießen, Bundesrepublik Deutschland
° Olech, Dr. B., Danilowskiego 1/20, 01-833 Warszawa, Poland
Oliveira, N. G., Rua da Boa Hora, 85, r/c, E, Porto 1, Portugal
Olney, P. J. S., Zoological Society, Regents Park, London NW1 4RY, United Kingdom
Olrog, Prof. C. C., Instituto Miguel Lillo, Miguel Lillo 205, 4000 Tucuman, Argentine
* de Olrog, Mrs. S. G. M. B.
° Olson, Dr. S. L., NHB E612, MRC 116, Smithsonian Institution, Washington, DC 20560, USA
Opdam, Dr. P., Research Institute for Nature Management, Kasteel Broekhuizen, Leersum, Netherlands
Oppermann, Dr. H., Fündlingsweg 8, 4600 Dortmund 50, Bundesrepublik Deutschland
* Orth, Mrs. G.

Ouellet, Dr. H., National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario K1A OM8, Canada

° Paakspuu, V., Jaamastreet 3-14, 203190 Lihula, Estonia, USSR
Papi, F., Istituto di Biologia Generale, Via A. Volta 6, 56100 Pisa, Italy
Paran, Y., 19 Barak Street, Tel Aviv 69933, Israel
* Paran, Mrs. E.
Parmelee, Dr. D. F., Chairman, Field Biology Program, University of Minnesota, 349 James Ford Bell Museum of Nat. History, 10 Church Street S. E., Minneapolis, MN 55455, USA
* Parmelee, Mrs. J. M.
Pauly, Frau T., Schussenrieder Str. 72, 7952 Bad Buchau, Bundesrepublik Deutschland
Pauwels, B., 42 rue Emile Collard, 4030 Grivegnee (Liege), Belgium
Peakall, D. B., Wildlife Toxicology Division, National Wildlife Research Centre, Ottawa, Ontario KIA 0E7, Canada
Pearson, D. L., 208 Life Sciences-Biology, Pennsylvania State University, University Park, PA 16802, USA
Pelle, I., Pančevačka 28, 23000 Zrenjanin, Yugoslavia
° Penev, Dr. D., Institut für Forstwissenschaften, Sofia Gische 15, Bulgaria
Pernoll, Prof. Dr. I., Pfeddersheimer Weg 2 a, 1000 Berlin 38, Bundesrepublik Deutschland
Perrins, Dr. C. M., Edward Grey Institute, Department of Zoology, South Parks Road, Oxford, United Kingdom
Perutz, Frl. K., ZiF, Universität Bielefeld, Wellenberg 1, 4800 Bielefeld, Bundesrepublik Deutschland
Peters, Dr. D. S., Forschungsinstitut Senckenberg, Senckenberg-Anlage 25, 6000 Frankfurt, Bundesrepublik Deutschland
* Peters, Frau Dr. M.
* Petersen, B. D., Skovfogedhuset, Snaptun, 8700 Horsens, Denmark
Petersen, P. C., 235 McClellan Boulevard, Davenport, Iowa 52803, USA
* Petersen, Mrs. M. L.
Peterson, Dr. R. T., 125 Neck Road, Old Lyme, Conn. 06371, USA
* Peterson, Mrs. R. T.
Pettke, H., Feldstr. 173, 2300 Kiel, Bundesrepublik Deutschland
* Pettke, Frau I.
° Peyton, L. J., Zoophysiologist, Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99701, USA
Phelps, W. H., Colección Ornitologica Phelps, Apartado 2009 Caracas 101, Venezuela
* Phelps, Mrs. K. D.
Phipps, G. R., 40 Hebe Street, Greenacre NSW 2190, Australia
Pitelka, Dr. F. A., Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA
Pohl, Dr. H., Max-Planck-Institut für Verhaltensphysiologie, 8131 Andechs, Bundesrepublik Deutschland
Pohl-Apel, Frau G., Universität Bielfeld, Lehrstuhl für Verhaltensphysiologie, Morgenbreede 45, 4800 Bielefeld 1, Bundesrepublik Deutschland
Possat, Dr. J., Fernkorngasse 43/1, 1100 Wien X, Österreich
Powell, G., Patuyent Wildlife Res. Center, U.S. Fish and Wildlife Service, Laurel, Md. 20811, USA
Prater, A. J., B.T.O., Beech Grove, Tring, Herts. HP23 5NR, United Kingdom
Prigogine, Dr. A., Av. des Volontaires 243, BT E 27, 1150 Bruxelles, Belgium
° Priklonski, Dr. S. G., Oka State Reserve, P.O. Lakash, Spasski R., Ryazan District, USSR
Procopé, N., M. Sc., Ehrensvärdsvägen 24-26 A 3, 00150 Helsingfors 15, Finland
Pröve, Dr. E., Lehrstuhl für Verhaltensphysiologie, Universität Bielefeld, Postfach 8640, 4800 Bielefeld 1, Bundesrepublik Deutschland
* Pröve, Frau R.
Pulliam, Dr. H. R., Tile Barn Cottage, Seaford Road, Alfriston near Polegate, East Sussex BN26 5TT, United Kingdom

* Pulliam, Mrs. J.

° Rabøl, J., Zoological Laboratory, Universitetsparken 15, 2100 Copenhagen, Denmark
Raethel, Dr. H. S., Xantener Straße 7, 1000 Berlin 15, Bundesrepublik Deutschland
Raiss, Frau R., Fachbereich Biologie (Zoologie) der Universität, AG P.Ö.V., Siesmayerstr. 70, 6000 Frankfurt, Bundesrepublik Deutschland
Rautenberg, Prof. Dr. W., Lehrstuhl für Tierphysiologie, Ruhr-Universität Bochum, Postfach 102148, 4630 Bochum 1, Bundesrepublik Deutschland
Redpath, Dr. T., Hahn-Meitner-Institut für Kernforschung, Bereich Strahlenchemie, Glienikker Str. 100, 1000 Berlin 37, Bundesrepublik Deutschland
Reed, Mrs. S. M., 4 Mamaku Street, Meadowbank, Auckland 5, New Zealand
Reid, J. B., Department of Psychology, University of St. Andrews, St. Andrews, Fife KY16 9AL, United Kingdom
Rheinwald, Dr. G., Zoologisches Forschungsinstitut, Adenauerallee 150—164, 5300 Bonn 1, Bundesrepublik Deutschland
Richards, Dr. S. A., Wye College, Ashford, Kent TN25 5AH, United Kingdom
Richardson, Dr. W. J., LGL Ltd., 44 Eglinton Ave. West, Toronto M4R IAI, Canada
* Richardson, Mrs. D. M.
Riggert, Dr. T. L., „Stonewall", Glen Road, 6070, Darlington, Western Australia
* Riggert, Mrs. C.
Ripley, S. D., Smithsonian Institution, Washington, D. C. 20560, USA
* Ripley, Mrs. M. L.
Risebrough, R., 142 Vicente Rd., Berkeley, Calif. 94705, USA
Robbins, C. S., Migratory Bird and Habitat Research Laboratory, U.S. Fish and Wildlife Service, Laurel, Maryland 20811, USA
Robertson, Dr. R. J., Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada
° Roche, J.-C., Aubenas-les-Alpes, 04110 Reillanne, France
Rödiger, K. S., Weislingen Str. 6—8, 1000 Berlin 28, Bundesrepublik Deutschland
Rogers, Dr. L., Pharmacology Department, Monash University, Clayton, Victoria 3168, Australia
Rogge, E.M.H., B. Sc., B.A., Bergvägen 46/48, 55280 Jönköping, Sweden
Ronchi, Mlle E., Universität Bielefeld, Postfach 8640, 48 Bielefeld, Bundesrepublik Deutschland
de Roos, Dr. G. T., Dorpsstraat 198, Vlieland, Netherlands
Rooth, Dr. J., R.I.N. — Broekhuizen, Leersum, Netherlands
Rosenthal, Mrs. E. S., 1212 Pine Ave. W-803, Montreal H3G IA9, P.Q., Canada
Rosner, Dr. G., Postf. 102148, Ruhr-Universität, Lehrstuhl für Tierphysiologie, 4630 Bochum-Querenburg, Bundesrepublik Deutschland
Rothe, H. J., Zoologisches Institut FB 16.4, Universität des Saarlandes, 6600 Saarbrücken, Bundesrepublik Deutschland
° Roux, Dr. F., C.R.B.P.O., 55 rue de Buffon, 75005 Paris, France
Rowley, I., C.S.I.R.O., Division of Wildlife Research, Clayton Road, Helena Valley W.A. 6056, Australia
* Rowley, Dr. E.
Rubel, Dr. E.W., Department of Otolaryngology, Box 430, University of Virginia, Medical Centre, Charlottesville, Va 22901, USA
Rüppell, Prof. Dr. G., Zoologisches Institut der Technischen Universität, Pockelsstr. 10 a, 3300 Braunschweig, Bundesrepublik Deutschland
Runnerström, B. G., Poststyrelsen, EK, 105 00 Stockholm, Sweden
° Rustamov, Prof. A., Academ. of AS TSSR, Turkmen. SSR, Pervomayskaya Str. 62, 744012 Ashkhabad 12, USSR
Rutschke, Prof., Dr. E., Rosenstr. 12, 1502 Potsdam-Babelsberg, Deutsche Demokratische Republik

Sachs, Dr. M. B., John Hopkins University, Sch. of Medicine, 506 Traylor Research Building, 720 Rutland Avenue, Baltimore, Maryland 21205, USA

Saiff, Dr. E., Ramapo College — Biology, 505 Ramapo Valley Rd., Mahwah, N.J. 07430, USA
von Saint Paul, Dr. U., Max-Planck-Institut für Verhaltensphysiologie, 8131 Andechs, Bundesrepublik Deutschland
Salomonsen, Prof. Dr. F., Zoologisches Museum, Universitetsparken 15, 2100 Kopenhagen Ø, Denmark
Sanft, Dr. K., Reinickendorfer Str. 74, 1000 Berlin 65, Bundesrepublik Deutschland
°* Saroso, M., P.O.B. 272/Kby., Kebayoran, Jakarta Selatan, Indonesia
Sauer, Prof. Dr. E. G. F., Adenauerallee 162, 5300 Bonn 1, Bundesrepublik Deutschland
Saunders, J. C., Ph. D., Department of Otorhinolaryngology, University of Pennsylvania, 3400 Spruce Str., Philadelphia, PA. 19104, USA
Saurola, P., Zoological Museum, Ringing Centre, P. Rautatiek. 13, 00100 Helsinki 10, Finland
* Saurola, Mrs. H.-I.
Scheich, Prof. Dr. H., Zoologisches Institut der Technischen Hochschule Darmstadt, Schnittspahnstr. 3, 6100 Darmstadt, Bundesrepublik Deutschland
Scheid, Dr. P., Max-Planck-Institut für experimentelle Medizin, Abt. Physiologie, 3400 Göttingen, Bundesrepublik Deutschland
Schenker, A., c/o Beck, Wenkenhaldenweg 26, 4125 Riehen, Schweiz
Scherner, Dr. E. R., Plauener Str. 7, 3400 Göttingen 1, Bundesrepublik Deutschland
Scherzinger, Dr. W., Guldensteig 7, 8351 Waldhäuser, Bundesrepublik Deutschland
Schifferli, Dr. A., Vogelwarte, 6204 Sempach, Schweiz
* Schifferli, Dr. L.
Schifter, Dr. H., Naturhistorisches Museum, Postfach 417, 1014 Wien, Österreich
* Schifter, Frau T.
Schmersow, K., Carmer Str. 10, 1 Berlin 12, Bundesrepublik Deutschland
Schmid, C. R., Jr., P.O.B. 71, North Truro, Mass. 02652, USA
°* Schmidt, B., Institut für Vogelforschung „Vogelwarte Helgoland“, 2940 Wilhelmshaven-Rüstersiel, Bundesrepublik Deutschland
Schmidt, Dr. I., MPI f. Physiol. und Klinische Forschung, W. G. Kerckhoff-Institut, 6350 Bad Nauheim, Bundesrepublik Deutschland
Schmidt, Dr. W., Apostelweg 9 B, 2000 Hamburg 73, Bundesrepublik Deutschland
Schmidt-Koenig, Prof. Dr. K., Abt. Verhaltensphysiologie, Beim Kupferhammer 8, 7400 Tübingen, Bundesrepublik Deutschland
Schneider, W., August-Bebel-Str. 45 I, 703 Leipzig S 3, Deutsche Demokratische Republik
Schölzel, Frau H., Thurgauer Str. 12, 1000 Berlin 51, Bundesrepublik Deutschland
Schoennagel, Dr. E., Meisenbrink 14, 3250 Hameln, Bundesrepublik Deutschland
* Schoennagel, Frau S.
Schreiber, Dr. R. W., Curator of Ornithology, Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007, USA
* Schreiber, Mrs. E. A.
Schröder-Bonhof, Frl. S., Argentinische Allee 3, 1000 Berlin 37, Bundesrepublik Deutschland
Schuchmann, K.-L., Fachbereich Biologie (Zoologie), Siesmayerstr. 70, 6000 Frankfurt, Bundesrepublik Deutschland
Schüz, Prof. Dr. E., Elmar-Doch-Str. 39, 7140 Ludwigsburg, Bundesrepublik Deutschland
* Schüz, Frau H.
Schuler, Dr. W., II. Zoologisches Institut und Museum der Universität, Berliner Straße 28, 3400 Göttingen, Bundesrepublik Deutschland
° Schuster, Mrs. A., Aloys-Schneider-Str. 14, 5530 Gerolstein, Bundesrepublik Deutschland
Schwabl, H., Vogelwarte Radolfzell/Obstberg, 7760 Radolfzell Möggingen, Bundesrepublik Deutschland
Schwartzkopff, Prof. Dr. J., Ruhr-Universität, Postfach 102148, 4630 Bochum 1, Bundesrepublik Deutschland
Schwarz, J., Sophie-Charlotten-Str. 112, 1000 Berlin 19, Bundesrepublik Deutschland
Schwarz, Dr. M., Elisabethenstr. 24, 4051 Basel, Schweiz

SEEL, Dr. D. C., Institute of Terrestrial Ecology, Penrhos Road, Bangor, Gwynedd, LL57 2LQ, United Kingdom
SEITZ, Dr. A., Jochensteinstr. 8, 8500 Nürnberg, Bundesrepublik Deutschland
° SENGUPTA, Dr. S., 15/1 Ramkali Mukherjee Lane, Calcutta 700050, India
°* SENILA-VASILIU, Mme M., Aleea Teilor, Bloc 2 C, Sc. B. I/4, 0300 Pitesti, Rumania
SERVENTY, Dr. D. L., 27 Everett Street, Nedlands, 6009, Western Australia
SHARP, Dr. P. J., ARC Poultry Research Centre, Kings Buildings, Edinburgh EH9 3JS, United Kingdom
SHARROCK, Dr. J. T. R., Fountains, Park Lane, Blunham, Bedford MK44 3NJ, United Kingdom
° SHEPPARD, J. M., Office of Endangered Species, U.S. Fish and Wildlife Service, Washington, D. C. 20240, USA
SHIELDS, G. F., Assist. Prof. Zool., Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99701, USA
* SHIELDS, Mrs. G. F.
SHORT, Prof. Dr. L. L., Ornithology, American Museum Nat. History, 79 St. and Central Park West, New York N.Y. 10024, USA
° SIBLEY, Prof. C. G., Peabody Museum of Nat. History, Yale University, New Haven, Conn. 06520, USA
°* SIBLEY, Mrs. C. G.
SICK, Dr. H., Academia Brasileira de Ciências, Caixa Postal 229, Rio de Janeiro, RJ, Brazil
SIEGFRIED, W. R., Fitzpatrick Institute, University of Cape Town, Rondebosch 7700, South Africa
SIELMANN, H., Am Gänsebühel 13, 8 München-Obermenzing, Bundesrepublik Deutschland
SIMBERLOFF, Dr. D., Department of Biological Science, Florida State University, Tallahassee, Florida 32306, USA
SIMON, Prof. Dr. E., MPI für Physiol. u. Klin. Forschung, W. G. Kerckhoff-Institut, 6350 Bad Nauheim, Bundesrepublik Deutschland
SIMON-OPPERMANN, Dr. C., MPI f. Physiol. u. Klin. Forschung, W. G. Kerckhoff-Institut, 6350 Bad Nauheim, Bundesrepublik Deutschland
SIMPSON, S. M., Department of Zoology, University College, Bangor, Gwynedd, United Kingdom
* SINGER, D., Institut für Vogelforschung, „Vogelwarte Helgoland“, 2540 Wilhelmshaven-Rüstersiel, Bundesrepublik Deutschland
SJÖLANDER, Dr. S., Biologie I, Universität Bielefeld, Postfach 8640, 4800 Bielefeld, Bundesrepublik Deutschland
SKADHAUGE, E., Panum Institute, 3 C Blegdamsvej, 2200 Copenhagen, Denmark
DA CAMARA SMEETS, M., Laboratoire Ecologie Animale, 5, Place de la Croix du Sud, 1348 Louvain La Neuve, Belgium
SMIES, M., Shell-Research, Sittingwourne, Kent ME9 8AG, United Kingdom
SMITH, Dr. N. G., Box 2072, Balboa, Canal Zone
SNOW, Dr. D. W., Zoological Museum, Tring, Hertfordshire, United Kingdom
* SNOW, Mrs. B. K.
SOMADIKARTA, Dr. S., Museum Zoologicum Bogoriense, Bogor, Indonesia
SOSSINKA, Dr. R., Verhaltensphysiologie, Universität Bielefeld, Postfach 8640, 4800 Bielefeld 1, Bundesrepublik Deutschland
SPANÒ, Dr. S., Istituto di Zoologia, Via Balbi 5, 16126 Genova, Italy
° SPENCER, R., c/o British Trust for Ornithology, Beech Grove, Tring, Hertfordshire HP23 5NR, United Kingdom
SPITZER, Dr. G., II. Zoologisches Institut der Universität, Dr. Karl Lueger-Ring 1, 1010 Wien, Österreich
°* STANLEY, B. L., York College of Pennsylvania, Country Club Rd., York, Pennsylvania 17405, USA
STARK, D. M., 2 Harland Road, Castletown, Thurso KW14 8UB, Caithness, Scotland, United Kingdom
STEIN, Dr. R. C., Department of Biology, State University College, 1300 Elmwood Avenue, Buffalo, N.Y. 14222, USA

Stein-von Spiess, Frau S., Auf dem Greite 18, 3400 Göttingen-Grone, Bundesrepublik Deutschland
Steinbacher, Prof. Dr. G., Siebentischstr. 60 a, 8900 Augsburg, Bundesrepublik Deutschland
* Steinbacher, Frau G.
Steinbacher, Dr. J., Forschungsinstitut Senckenberg, Senckenberg Anlage 25, 6000 Frankfurt, Bundesrepublik Deutschland
* Steinbacher, Frau E.
Sternberg, H., Im Schapenkampe 11, 3300 Braunschweig, Bundesrepublik Deutschland
Stettenheim, Dr. P., Meriden Road, Lebanon, New Hampshire 03766, USA
Stiles, Dr. F. G., Escuela de Biologîa, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica, C. A.
Stokkan, K. A., Institute of Medical Biology, Physiological Section, University of Tromsø, 9001 Tromsø, Norway
Stork, Dr. H. J., Institut für Allgemeine Zoologie der Freien Universität Berlin, Königin-Luise-Str. 1—3, 1000 Berlin 33, Bundesrepublik Deutschland
Stresemann, Frau V., Kamillenstr. 28, 1000 Berlin 45, Bundesrepublik Deutschland
Sunkel, Frau M., Am Galgenberg 15, 6413 Tann/Rhön, Bundesrepublik Deutschland
Suter, W., Else Züblin-Str. 3, 8047 Zürich, Schweiz
Sutter, Dr. E., Naturhistorisches Museum, Augustinergasse 2, 4051 Basel, Schweiz
* Sutter, Frau G.
Švehlik, Dr. J., Vojenská 4, 04001 Košice, Czechoslovakia
Swennen, C., Netherlands Institute for Sea Research, P.O.B. 59, Den Burg-Texel, Netherlands
Sykes, Dr. A. H., Wye College, Ashford, Kent TN25 5AH, United Kingdom
* Sykes, Mrs. M.
Szijj, Dr. L. J., Department of Biological Sciences, California State Polytechnic University, Pomona, CA 91768, USA

Taapken, Dr. H. J., Utrechtseweg 43, 1213 TL Hilversum, Netherlands
Tahon, I. J., Station de Zoologie Appliquée, Chemin de Liroux 8, 5800 Gembloux, Belgium
Takahashi, J., Department of Zoology, University of Texas at Austin, Austin, TX 78712, USA
Temple Lang, J., Legal Service, EEC Commission, 200 Wetstraat, 1049 Brussels, Belgium
* Temple Lang, Mrs. L.
Terborgh, Prof. J. W., Department of Biology, Princeton University, Princeton, N.J. 08540, USA
Terschuren, Mrs. J. A., av. de la Charmille 8, Bte. 2, 1200 Brussels, Belgium
Thaler, Dr. E., Institut für Zoologie der Universität, Universitätsstr. 4, 6020 Innsbruck, Österreich
° Thapliyal, Prof. J. P., Department of Zoology, Banaras Hindu University, Varanasi 221005, India
Thiede, Dr. W., Fliederstr. 2, 4280 Borken, Bundesrepublik Deutschland
* Thiede, Frau Dr. U.
Thielcke, Dr. G., Storchenweg 1, 7760 Radolfzell-Möggingen, Bundesrepublik Deutschland
Thimm, Dr. F., Physiologisches Institut der Sporthochschule, Carl-Diem-Weg, 5000 Köln 41, Bundesrepublik Deutschland
Thiollay, Dr. J. M., 59 rue des Capucines, 92370 Chaville, France
Thomas, Dr. D. H., Department of Zoology, University College, Cardiff CF 1 XL, United Kingdom
° Tiainen, J., University of Helsinki, Lammi Biological Station, 16900 Lammi, Finland
Titman, Dr. R. D., P.O.B. 40, Macdonald College, Ste. Anne de Bellevue, Québec HOA 1CO, Canada
* Titman, Mrs. E.
Todd, F. S., Senior Research Fellow, Hubbs/Sea World Research Institute, 1700 South Shores Road, San Diego, CA 92109, USA
Todt, Prof. Dr. D., Haderslebenerstr. 9, 1000 Berlin 41, Bundesrepublik Deutschland

Tomiałojc, Dr. L., Museum Nat. History, Wrocław University, u. Sienkiewicza 21, 50-335 Wrocław, Poland
Tousey, Miss K., 18 Western Ave., Essex, Mass. 01929, USA
Traylor, M. A., Jr., Field Museum of Natural History, Roosevelt Rd. at Lake Shore Dr., Chicago, Illinois 60605, USA
* Traylor, Mrs. M.
Trent Thomas, Miss B., Partado 80844, Caracas 108, Venezuela
Turek, F. W., Department of Biological Sciences, Northwestern University, Evanston, Illinois 60201, USA
* Tu-ton, Mme J., Aubenas-les-Alpes, 04110 Reillanne, France
Tutman, Prof. I., Iva Vojnovića 72, 50000 Dubrovnik 3, Yugoslavia

Ulfstrand, Prof. S., Department of Animal Ecology, Ecology Building, 223 62 Lund, Sweden
°* Ulfstrand, Mrs. A.

Vasić, V. F., Institute for Biological Research, 29. Novembra 142, 1060 Beograd, Yugoslavia
Vasiliu, Prof. Dr. D. G., Aleea Teilor, Bloc 2 C, Sc. B. I/4, 0300 Pitesti, Rumania
Vehrencamp, Dr. S. L., Department of Biology C-016, University of Calif. San Diego, La Jolla, CA 92093, USA
° Verheyen, Prof. Dr. R. F., Universitaire Instelling Antw., Departement Biologie, Universiteitsplein 1, 2610 Wilrijk, Belgium
Veselovský, Prof. Dr. Z., Zoological Garden-Troja 120, 17100, Czechoslovakia
° Viehmann, W., Dipl. Biol., Johann-Wolfgang-Goethe-Universität, Siesmayerstr., 6000 Frankfurt 1, Bundesrepublik Deutschland
° Viht, E., Eesti Metseinstituut Rôõmu tee 2, 202400 Tartu, Estonian SSR, USSR
Vinokurov, Mr. A., Central Laboratorium für Naturschutz, 142790 Moskau reg. P.O. Vilar, USSR
Violani, Dr. C., Istituto di Ecologia Animale ed Etologia, Università (Pal. Botta), 27100 Pavia, Italy
* Violani, Mrs. G.
* Violani, G.
Visalberghi, Dr. E., Via Spalato 11, 00198 Roma, Italy
Voous, Prof. Dr. K. H., v. d. D. van Maasdamlaan 28, Huizen, N.H., Netherlands
* Voous-Luiting, Mrs. H. C.
Vuilleumier, Dr. F., American Museum of Natural History, Central Park West at 79th Street, New York, N.Y. 10024, USA

Walcott, C., Department of Biology, State University of New York, Stony Brook, N.Y. 11794, USA
Wallraff, Dr. H. G., Max-Planck-Institut, 8131 Seewiesen, Bundesrepublik Deutschland
Walmsley, J. G., Station Biologique, La Tour du Valat, Le Sambuc, 13200 Arles, France
Walsberg, Dr. G. E., Department of Zoology, Washington State University, Pullman, Washington 99164, USA
Walter, Prof. Dr. H., Department of Geography, University of California, Los Angeles, CA 90024, USA
Warham, Dr. J., Zoology Department, University of Canterbury, Christchurch I, New Zealand
Wartmann, Dipl.-Nat. B. A., Paradiesstr. 24, 8802 Kilchberg, Schweiz
Watson, Dr. G. W., Curator, National Museum of Natural History, Smithsonian Institution, Wahington, D. C. 20560, USA
Wattel, Dr. J., Zoölogisch Museum, Postbus 20125, 1000 HC Amsterdam, Netherlands
Weathers, Dr. W. W., Department of Avian Sciences, University of California, Davis, CA 95616, USA
Weber, Dr. A., Hospitalstr. 11, 625 Limburg/Lahn, Bundesrepublik Deutschland
Weise, Prof. Dr. H.-J., Händelweg 3, 1000 Berlin 21, Bundesrepublik Deutschland
Weiss-Kreis, Dr. W., Mostackerstr. 11, 4051 Basel, Schweiz

* Weiss-Kreis, Frau R.
Welty, Prof. J. C., Route 1, Beloit, Wisconsin 53511, USA
Wendland, Dr. V., Ringbahnstr. 79, 1 Berlin 42, Bundesrepublik Deutschland
* Wendland, Frau R.
Westerskov, Prof. Dr. K. E., Department of Zoology, University of Otago, Dunedin, New Zealand
Westerterp, Dr. K. R., Department of Biology, University of Stirling, Stirling FK9 4LA, Scotland, United Kingdom
Weston, Mrs. I. L., P.O.B. 249, Port Moresby, Papua New Guinea
* Weston, T. M.
White, Prof. Dr. C. M., Department of Zoology, Brigham Young University, Provo, Utah 84602, USA
Whitmore, Mrs. M., 6034 Hall Street, Grand Rapids, Michigan, USA
Wickler, Dr. W., Max-Planck-Institut für Verhaltensphys., 8131 Seewiesen, Bundesrepublik Deutschland
Wiens, Dr. J. A., Department of Zoology, Oregon State University, Corvallis, Oregon 97331, USA
Williams, Mrs. C. M., 2 Jean St., Nelly Bay, Magnetic Island, Queensland 4816, Australia
Willis, E. O., Avenida Modesto Fernandes 5/n, Barão Geraldo, 13100 Campinas, SP, Brazil
°* Willis, Mrs. Y. O.
Wilson, Prof. A. C., Department of Biochemistry, University of California, Berkeley, CA 94720, USA
Wilson, H. I., Forest and Wildlife Service, Sidmonton Pl., Bray, Co. Wicklow, Ireland
Wiltschko, W., FB Biologie der Universität, Zoologie, Siesmayerstr. 70, 6000 Frankfurt, Bundesrepublik Deutschland
* Wiltschko, Frau R.
Wingfield, Dr. J. C., Department of Zoology, University of Washington, Seattle, Washington 98195, USA
Wink, M., Institut für Pharmazeutische Biologie der Technischen Universität, Pockelsstr. 4, 3300 Braunschweig, Bundesrepublik Deutschland
* Wink, Frau C.
Winkel, Dr. W., Außenstation Braunschweig für Populationsökologie beim Institut für Vogelforschung „Vogelwarte Helgoland“, Bauernstr. 14, 3302 Cremlingen 1, Bundesrepublik Deutschland
* Winkel, Frau D.
° Winkler, Dr. H. C., Oberweiden 37, A-2295 Oberweiden, Österreich
°* Winkler, Frau
Winterbottom, Dr. J., 9 Alexandra Avenue, Oranjezicht, Cape Town, 8001, South Africa
* Winterbottom, Mrs. M. C.
Witt, Dr. K., Tietzenweg 81, 1000 Berlin 45, Bundesrepublik Deutschland
* Witt, Frau Dr. J.
Wittenberg, Dr. J., Maienstr. 13, 3300 Braunschweig, Bundesrepublik Deutschland
Wolf, Dr. L. L., Department of Biology, Syracuse University, Syracuse, N.Y. 13210, USA
Wolffgramm, Dr. J., Physiologisches Institut des Universitätsklinikums, Hufelandstr. 55, 4300 Essen 1, Bundesrepublik Deutschland
Wolters, Dr. H. E., Zool. Museum Alexander Koenig, Adenauerallee 150—164, 5300 Bonn 1, Bundesrepublik Deutschland
Woolfenden, G. E., Department of Biology, University of South Florida, Tampa, Fl. 33620, USA
Wooller, Dr. R., School of Life Sciences, Murdoch University, Western Australia 6153
* Wothe, C., Institut für Vogelforschung, Vogelwarte Helgoland, 2940 Wilhelmshaven-Rüstersiel, Bundesrepublik Deutschland
Würdinger, Dr. I., Pädagogische Hochschule, 3200 Hildesheim, Bundesrepublik Deutschland
Wüst, Dr. W., Hohenlohestr. 61, 8000 München 19, Bundesrepublik Deutschland
* Wüst, Frau I.
° Wunderlich, Dr. K., Karolinenhofweg 6, 1187 Berlin, Deutsche Demokratische Republik

Wyndham, E., A. E.S., Griffith University, Nathan, Qld. 4111, Australia

Yokoyama, Dr. K., Department of Zoology, University of Texas at Austin, Austin, TX 78712, USA

Yoshii, M., Bird Migration Research Center, Yamashina Institute for Ornithology, 8-20 Nampeidai-machi, Shibuya-ku, Tokyo 150, Japan

° Zhordania, Dr. R. G., State University, Tbilisi 28, Georgia, USSR

Zimdahl, Dr. W., Otto-Nuschke-Str. 28, 110 Berlin, Deutsche Demokratische Republik

Zink, Dr. G., Dürrenhofstr. 16, 7760 Möggingen, Bundesrepublik Deutschland

Ziswiler, Prof. Dr. V., Universität, Zoologie, Künstlergasse 16, 8006 Zürich, Schweiz

Zwarts, L., Achterwei 23, EE (FRL), Netherlands

Zweers, Dr. G. A., Department of Morphology, Zoölog. Lab., Kaiserstr. 63, Leiden, Netherlands

* Zweers, Mrs. T.

Der XVII. Internationale Ornithologen-Kongreß in Berlin

Rolf Nöhring

Vorbereitungen

Weit über ein halbes Jahrhundert sei verstrichen, seit ein Internationaler Ornithologen-Kongreß in Deutschland abgehalten wurde, und die Deutsche Ornithologen-Gesellschaft befinde sich tief in der Schuld aller früheren Gastgeber — damit empfahl Günther Niethammer beim Ausscheiden aus dem Präsidentenamt der DO-G seinem Nachfolger, in Canberra eine Einladung auszusprechen.

Dort nahm das Internationale Ornithologische Komitee die Einladung nach Deutschland an und wählte Herrn Prof. Dr. Donald S. Farner aus Seattle, Washington, U.S.A., zum Präsidenten. Die deutschen Mitglieder dieses Komitees ernannten mich zum General-Sekretär, und ich bestimmte Berlin zum Tagungsort, auf die Hilfe der Stadtväter und des Zoologischen Gartens vertrauend, der schon 1910 den V. Internationalen Ornithologen-Kongreß beherbergt und nachhaltig gefördert hatte.

Der Präsident berief einen Ausschuß für das Wissenschaftliche Programm, der — die neuen Statuten vorwegnehmend — je zur Hälfte aus Vertretern des Gastlandes und aus Ornithologen anderer Länder bestand. Herr Prof. Dr. Klaus Immelmann übernahm dessen Vorsitz und wurde bald zum spiritus rector des Wissenschaftlichen Programmes. Für das Film-Programm stellte sich Herr Prof. Dr. Georg Rüppell zur Verfügung. Der Generalsekretär arbeitete die Exkursionen aus.

Ein international zusammengesetzter Ausschuß mußte weniger beweglich sein als ein örtliches Gremium. Er trat darum nur dreimal zusammen und stets unvollständig. Im Oktober 1975 wurden in Berlin der allgemeine Programmablauf festgelegt, die Themata der Symposia bestimmt und die um ihre Mitwirkung zu bittenden Plenarredner ausgewählt. Im September 1976 in Kiel ergänzte der Ausschuß das Programm und legte Ende Februar 1978 in Berlin den endgültigen zeitlichen und räumlichen Ablauf fest.

Im ersten Quartal 1976 erschien in fast allen bedeutenden ornithologischen Zeitschriften eine Erste Ankündigung des Kongresses. Die daraufhin eingehenden Interessebekundungen wurden im Dezember 1976 mit einer ausführlichen Zweiten Ankündigung beantwortet, der eine Karte für eine vorläufige Anmeldung beilag. Hiermit meldeten sich 1 093 Personen zum Kongreß und 525 Personen für die Exkursionen vor (259) und nach (266) dem Kongreß an.

Im November 1977 wurde, zusammen mit den Unterlagen für eine endgültige Anmeldung, die Dritte und Letzte Ankündigung verschickt. Der Generalsekretär bot darin seine Hilfe an bei der Reservierung von Unterkünften während des Kongresses in Berlin. Verkehrsämter pflegen Kongreßteilnehmer über die ganze Stadt zu verstreuen; wir wollten aber unsere Gäste auch außerhalb der Veranstaltungen möglichst nahe beieinander sein lassen, um so persönliche Verbindungen knüpfen oder festigen zu können.

Es meldeten sich 780 Teilnehmer endgültig an, 633 Ordentliche und 147 Außerordentliche Mitglieder. Davon waren 73 Mitglieder am Erscheinen verhindert. Nach

ihrer Herkunft verteilten sich die anwesenden 707 Mitglieder auf die folgenden 38 (43) Länder (in Klammern die vorläufig angemeldeten Teilnehmer): Argentinien 2 (4), Australien 23 (35), Belgien 20 (24), Bulgarien 0 (5), Brasilien 4 (4), Canal Zone 1 (1), Costa Rica 1 (0), Dänemark 12 (26), Bundesrepublik Deutschland 235 (358), Deutsche Demokratische Republik 9 (6), England 64 (74), Finnland 6 (16), Frankreich 22 (22), Holland 22 (35), Hongkong 0 (1), Indien 0 (7), Indonesien 1 (6), Iran 0 (1), Irland 2 (2), Island 0 (1), Israel 4 (5), Italien 12 (16), Japan 5 (4), Jugoslawien 4 (3), Kanada 26 (40), Kenia 0 (1), Mexiko 0 (1), Neuseeland 5 (20), Norwegen 3 (4), Österreich 11 (19), Papua-Neuguinea 2 (4), Polen 4 (8), Portugal 1 (1), Rhodesien 0 (2), Rumänien 2 (0), Sambia 1 (1), Schweden 16 (28), Schweiz 25 (37), Senegal 2 (2), Spanien 2 (8), Sowjetunion 4 (20), Südafrika 11 (17), Südwestafrika 0 (2), Tschad 1 (2), Tschechoslowakei 4 (6), Ungarn 0 (2), Venezuela 5 (4), Vereinigte Staaten von Amerika 136 (212).

Ein wesentlicher Grund für den großen Unterschied zwischen der angekündigten und der tatsächlichen Teilnahme am Kongreß lag sicherlich in dem stetig sinkenden Wechselkurs des US-Dollars von etwa DM 2,50 im Jahre 1976 auf knapp DM 2,00 bei Anmeldeschluß am 1. März 1978; dadurch waren die Kosten für Dollarbesitzer um ein Viertel gestiegen. Unabhängig hiervon mag auch mancher Interessierte die erhofften Genehmigungen oder Kostenzuschüsse nicht erhalten haben.

Die in Berlin eintreffenden Teilnehmer wurden vom Kongreßbüro empfangen. Heute ist die Meinung weit verbreitet, Studenten ließen sich nur noch gegen hohe Vergütung für die sogenannten Hilfsdienste gewinnen, wie sie solch ein Büro verlangt. Herr Prof. DIETMAR TODT degradierte diese Meinung zum Gerücht: er wußte seine Schüler für diese mühsame und für die Atmosphäre einer Zusammenkunft so wichtige Aufgabe zu begeistern. Den Damen ELKE BRÜSER, HENRIKE HULTSCH, ELETTRA RONCHI, SOPHIE SCHRÖDER-BONHOFF und UTE VON WENDENBURG und den Herren FERN DUVALL, DANIEL ESCHER-GRÄUB, DIETMAR HEIKE und BERND JÄNICKE danke ich für ihre umsichtige und liebenswürdige Betreuung der Teilnehmer. Meine Assistentin Frau INGEBORG BUJOK war nicht nur für finanzielle Belange verantwortlich; sie hatte auch für 360 Teilnehmer wunschgemäß Unterkunft bereitgestellt, davon für über 200 in vier nahe beieinander gelegenen Hotels, in die die Gäste vom Kongreßbüro weitergeleitet wurden.

Die Finanzierung des Kongresses konnte dank der großzügigen Hilfe des Senates von Berlin, vertreten durch den Senator für Wissenschaft und Forschung, gesichert werden. Die Deutsche Forschungsgemeinschaft trug auch etwas zu den Kongreßkosten bei, verhinderte aber jede Simultanübersetzung (die Eröffnungssitzung konnte dennoch zweisprachig gehört werden). Von den Ordentlichen Mitgliedern wurde eine Kongreßgebühr von DM 300 erhoben, die Außerordentlichen Mitglieder bezahlten DM 80. Einigen Referenten wurde ein Beitrag zu ihren Reisekosten gewährt. Entscheidende materielle und personelle Unterstützung erfuhr der Kongreß vom Zoologischen Garten Berlin; dem Aufsichtsrat und dessen Vorsitzendem, Herrn DIETRICH VON GRUNELIUS, und meinen Kollegen im Vorstand, Prof. Dr. HEINZ-GEORG KLÖS und Dr. HANS FRÄDRICH, sei dafür warmer Dank gesagt.

Der Kongreß fand in der Berliner Kongreßhalle statt, einem 1957/58 nach den Plänen des amerikanischen Architekten HUGH A. STUBBINS errichteten Bau, in dem sich

Kühnheit der Konstruktion mit Anmut der Erscheinung auf das Glücklichste verbinden. Neben dem großen Saal für die Plenarsitzungen und Filmvorführungen standen vier Räume für die gleichzeitig abzuhaltenden Symposia und ausreichend Zimmer für Gruppengespräche und Konferenzen zur Verfügung. Die 141 Tafelvorträge konnten geschlossen in einer Halle dargeboten werden. Die Eingangshalle, das (nicht von allen Teilnehmern gelobte) Restaurant und vielerlei Nebenräume boten Gelegenheit zu privaten Gesprächen. Die Kongreßhalle ist eingebettet in einen großen Park, und manche fachliche Auseinandersetzung fand ihren Ausklang auf Spaziergängen durch diese Anlagen. Mindestens der auf biologischem Gebiet tätige Wissenschaftler möchte keineswegs tagelang künstlich belüftet und belichtet werden; er weiß Sonnenschein und den Blick auf Wiesen und Bäume auch während der Kongreßarbeit sehr wohl zu schätzen.

Das wissenschaftliche Programm

Die Eröffnungssitzung begann am Montag, dem 5. Juni, 10.00 Uhr, im Großen Saal der Kongreßhalle, der geschmückt war mit den Portraitbildnissen der beiden bedeutendsten Berliner Ornithologen: OSKAR HEINROTH und ERWIN STRESEMANN. Die Deutsche Ornithologen-Gesellschaft begrüßte ihre Gäste durch ihren Präsidenten, Herrn PROF. IMMELMANN. Herr Senatsdirektor Prof. HARTMUT JÄCKEL überbrachte Willkommen und Grüße des Senates von Berlin. Der Generalsekretär erzählte von dem Beginn der Internationalen Ornithologen-Kongresse 1884 in Wien und 1891 in Budapest. Dann erklärte der Präsident des Kongresses, Herr Prof. DONALD S. FARNER, mit einer kurzen Adresse die Verhandlungen für eröffnet und bat Herrn Prof. KONRAD LORENZ zu seiner Gedächtnisrede auf OSKAR HEINROTH, die in diesem Bande auf Seite 83 nachzulesen ist.

Am Montagnachmittag setzte die vielfältige Arbeit des Kongresses ein mit acht gleichzeitig ablaufenden Veranstaltungen: vier Symposia und zwei Gruppengespräche wurden abgehalten, das Filmprogramm und die Tafelvorträge dargeboten. Dabei war Bedacht darauf gelegt, verwandte Themata nicht gleichzeitig zu behandeln. Die dadurch bedingte Vielfalt macht einen chronologischen Bericht über den Ablauf des Kongresses unsinnig. Wer sich aus historischen oder persönlichen Gründen für das Neben- und Nacheinander der Veranstaltungen interessiert, findet auf den Seiten 1437—1442 dieses Bandes die aus dem Programm übernommenen Tagesübersichten nachgedruckt. Ich beschränke mich auf wenige zusammenfassende Bemerkungen.

Jeder Arbeitstag begann mit einem etwa einstündigen Plenarvortrag, in dem der Wissensstand eines Fachgebietes zusammengefaßt oder Entwicklungslinien nachgezeichnet wurden. Die Plenarvorträge wurden nicht diskutiert.

Von den insgesamt 36 Symposia mußten je vier gleichzeitig abgehalten werden. Über den Inhalt der Vorträge unterrichtete eine Broschüre mit 198 Kurzfassungen. Der Präsident und der Ausschuß für das wissenschaftliche Programm hatten die Symposionsleiter ausgewählt; diese Leiter luden ihrerseits die Redner ihres Symposions ein. Im Durchschnitt trugen etwa fünf Redner pro Symposion vor. Kein Redner konnte aus eigener Initiative, also ohne Einladung, auf einem Symposion vortragen. Es ist gegen dieses System eingewandt worden, der einladende Leiter könne Vortragende mit kontroversen Ansichten (zur Auffassung des Leiters oder zur herrschenden Meinung) vorsätzlich ausschließen. Selbst wenn in Einzelfällen solch ein Verdacht gegeben sein mag,

so stehen dem doch unübersehbare Vorteile gegenüber: Von der Unbill durch jene Redner, die mit vielen Worten nichts oder nur sattsam Bekanntes zu sagen haben, bleibt das Auditorium verschont. Und: Unter engen Fachkollegen erreicht die Diskussion ein höheres und zuweilen höchstes Niveau. Leider kann sich von den Diskussionen in diesem Bande kein Niederschlag finden.

In noch höherem Ausmaß gilt das für die Gruppengespräche, in denen Detailfragen, während der Symposia nur flüchtig berührt, im gleichen oder kleineren Kreis vertieft wurden. Diese Gespräche leben von der spontanen Äußerung, die sich nicht schriftlich festhalten läßt. So steht in diesem Bande als programmatische Kurzfassung nur, was die Initiatoren gewollt haben, nicht aber, was geschehen ist.

Vor nicht geringere Schwierigkeiten sieht sich der Chronist gestellt, wenn er über das Filmprogramm berichten möchte. So wie sich akustisches Geschehen kaum einem anderen Sinnesorgan als dem Ohr eindeutig vermitteln läßt — was in den Symposia zur Bioakustik immer wieder, wenn auch zuweilen bewußt bagatellisiert, zum Ausdruck kam —, so läßt sich die optische Darbietung nur unzureichend beschreiben. Jene Filme, die in schönen Bildern die Eingriffe des Menschen in die Natur bewegt beklagen und auch keinen Ausweg zeigen, waren erfreulich gering vertreten. Meistens verband sich saubere, zuweilen künstlerische Kameraführung mit klarer wissenschaftlicher Aussage. Die mühevolle Auslese aus einem sehr umfangreichen Material hat sich gelohnt. Herrn Prof. Georg Rüppell, der Auswahl, Programm und Darbietung allein verantwortete und bewältigte, gebührt Dank und Anerkennung.

Neu für die Internationalen Ornithologen-Kongresse waren die Tafelvorträge, die sich als wertvoller Teil des wissenschaftlichen Programms erwiesen haben. Hier scheint sich ein eleganter und nutzbringender Ausweg aufzutun aus einigen Schwierigkeiten, die große Kongresse zunehmend belasten. Es könnte ein Weg sein zurück aus dem Massenbetrieb und hin zu intensiven Gesprächen unter wenigen wirklich Interessierten. Sehr spezielle Themata können hier uneingeschränkt besprochen werden. Der in der Diskussion vor einem hundertköpfigen Auditorium mit seiner Frage zögernde Teilnehmer verliert im kleinen Kreis seine — zuweilen auch sprachlichen — Hemmungen. Aber auch der Vortragende ohne Rednergabe ist seiner Schwierigkeiten enthoben. Und schließlich: Es ist begreiflich, daß Institute und Behörden Urlaub und Zuschüsse zum Kongreßbesuch ihren Mitarbeitern nur gewähren wollen, wenn diese die Institutsarbeit in einem Vortrag dem Kongreß vorstellen. Dieser Zwang zum Reden kann in Form des Tafelvortrages ungünstigstenfalles unschädlich für die Zeit und Aufmerksamkeit der Teilnehmer abgeleitet werden, bei kluger Themenwahl und Beschränkung auf Kernfragen sich aber zu einem wertvollen Beitrag entwickeln. Voraussetzung ist allerdings, daß die Institute das mancherorts anzutreffende törichte Vorurteil fahren lassen, ein Tafelvortrag sei kein ernsthafter Kongreßbeitrag. Als weitere Voraussetzung müssen die Kongreßleiter ausreichend große, gut beleuchtete und vor allem ruhige Räume zur Verfügung stellen. Tafelvorträge gehören nicht in abgelegene Flure und auch nicht wie Reklameplakate zwischen Fenster und Türen einer Durchgangshalle.

Das hier kurz skizzierte wissenschaftliche Programm hat, zusammen mit dem Präsidenten und dem zuständigen Ausschuß, Herr Prof. Immelmann entworfen und durchgeführt. Für seine geistige und organisatorische Leistung und für seine nie erlahmende Umsicht schuldet der Kongreß ihm großen Dank.

Exkursionen während des Kongresses

An fünf Arbeitstagen des Kongresses führten wissenschaftliche Zoomitarbeiter morgens vor Beginn der Verhandlungen durch die Vogelsammlung des Zoologischen Gartens. Diese Führungen fanden ebenso regen Zuspruch wie die von Herrn HINRICH ELVERS geleiteten Morgenspaziergänge durch den Tiergarten, die vor allem den Teilnehmern aus Übersee Gelegenheit geben sollten zum ersten Beobachten der häufigeren Parkvögel.

Der Donnerstag (8. Juni) war frei von wissenschaftlichen Veranstaltungen. Dieser Tag sollte zum Atemholen dienen nach und vor jeweils drei Kongreßtagen mit dichtgedrängtem Programm, zum persönlichen Gespräch und zum Kennenlernen der Stadt. Er sollte aber auch ein wenig einführen in Berlin-typische biologische Fragen.

Am frühen Donnerstagmorgen um 3.30 Uhr trafen sich die Teilnehmer auf dem Wittenbergplatz und wurden mit Autobussen zu den Zielen ihrer Morgenexkursionen gebracht: in den Volkspark Glienicke unter der Leitung von Dr. HARTMUT EBENHÖH, in den Botanischen Garten und an die Grunewaldseen (Dr. SIEGFRIED KANOWSKI), in den Tegeler Forst (JÜRGEN HINDEMITH und HANS-GÜNTER WILLE), an das Tegeler Fließ (Dr. HANS-JÜRGEN STORK und HANS-ULRICH HOFFMANN), zum Teufelsberg (HINRICH ELVERS), nach Tiefwerder und Pichelswerder (Dr. KLAUS WITT und Dr. HORST KOWALSKY), auf die Rieselfelder in Gatow (JOCHEN SCHWARZ) und in den Spandauer Forst (Dr. DIETER WESTPHAL). Die Gesamtleitung lag in den Händen von Herrn Dr. WITT. Neben einem mehr kursorischen Blick auf die hiesige Ornis wurden den Teilnehmern die oekologischen Gegebenheiten in einer von ihrer Umgebung radikal abgeschnittenen Stadt vorgestellt.

Am Donnerstagvormittag ließen sich etwa 300 Kongreßmitglieder von Herrn Prof. KLÖS, Herrn Dr. FRÄDRICH und ihren Assistenten ausgiebig durch den Zoologischen Garten führen. Außer den allmorgendlich vorgestellten Vogelsammlungen fanden die in den letzten Jahren errichteten Gebäude und Gehege für Säugetiere lebhaften Anklang.

Die in der seenartig erweiterten Havel gelegene Pfaueninsel war am Donnerstagnachmittag das Ziel eines Ausfluges, der mehr als 200 Mitglieder vereinte. Eine so zahlreich besuchte Unternehmung fördert naturgemäß mehr den persönlichen Kontakt. Dennoch gelang es der geschickten Führung der Herren JÜRGEN KLAWITTER, Dr. VICTOR WENDLAND und THOMAS GREGOR, auch ornithologische Leckerbissen vorzuzeigen, so den Zwergschnäpper *Ficedula parva*.

Gesellige Veranstaltungen

Zu einer Vorführung historischer Tänze hatte der Generalsekretär am Freitagabend (9. Juni) in die Kongreßhalle eingeladen. Das Ensemble Historischer Tanz Berlin, Hochschule der Künste, stellte in einer begeisternd schönen Aufführung — unter der Leitung von Herrn Prof. TAUBERT und zusammen mit dem Collegium Instrumentale Berlin — Tänze des 16. bis 19. Jahrhunderts in Originalkostümen vor. Die stark besuchte und mit lebhaftem Beifall aufgenommene Veranstaltung leitete der Generalsekretär ein mit Betrachtungen über den Zusammenhang von Kultur und Wissenschaft. Er definierte Kultur als einen zum Überleben nicht notwendigen Überschuß, der auf

bewußten oder unbewußten Spielregeln (Konvention) beruhe. Wo diese Spielregeln mißachtet oder vergessen werden, sterbe auch alle Kultur — überlebt werde nur noch biologisch.

Der Abschlußabend vereinte etwa 150 Gäste im Hotel Schweizerhof. Nun aller Verpflichtungen ledig, entspannten sich die Kongreßteilnehmer an einem berolinensischen Buffet und zeitgenössischem Tanz. Baron von Haartman dankte am Schlusse dem Senat von Berlin und der Stadt für die Gastfreundschaft und den Ausrichtern für die wissenschaftliche und organisatorische Vorbereitung und Durchführung des Kongresses. Berlin kennt keine Polizeistunde, und so wurde es spät, bis sich die letzten Gäste in angeregter und fröhlicher Stimmung voneinander trennten.

Auswärtige Exkursionen vor und nach dem Kongreß

Einer kritischen Betrachtung bedürfen die so umfangreich angebotenen auswärtigen Exkursionen vor und nach dem Kongreß. An den ursprünglich 18 (später nur noch 13) vorbereiteten mehrtätigen Exkursionen vor dem Kongreß, zu denen sich 259 Teilnehmer vorläufig angemeldet hatten, wollten nur 71 Personen endgültig teilnehmen, so daß 8 Exkursionen gestrichen werden mußten. Für die 20 (14) Exkursionen nach dem Kongreß lagen 266 vorläufige, aber nur 57 endgültige Anmeldungen vor; hier fielen 9 Exkursionen aus.

Der mancherseits erhobene Vorwurf, die hier aufgewendete Mühe — vor allem für die dann nicht durchgeführten Unternehmungen — sei viel zu groß gewesen, trifft zweifellos zu. Für künftige Kongresse mag ein Blick auf die möglichen Gründe nützlich sein. Der Unterschied zwischen vorläufigen und endgültigen Anmeldungen dürfte zum Teil in dem bereits erwähnten Wechselkursverfall des Dollars liegen. Meine leichtfertige Gutgläubigkeit an den Wert einstweiliger Interessebekundungen kommt wohl hinzu. Ein amerikanisches Reisebüro stiftete mit unautorisierten und überdies falschen Ankündigungen etliche Verwirrung unter den Interessenten aus den Vereinigten Staaten. Ein weiterer Grund könnte in der Ausweitung der Exkursionsziele über die Grenzen des gastgebenden Landes hinaus auf ganz Europa liegen: die weiten Anreisewege erhöhen die Kosten. Andererseits liegen die meistinteressierenden und dann auch meistbesuchten Ziele extrem peripher: Südspanien, Donaudelta, Lappland; in Deutschland fanden sich ausreichend Teilnehmer nur für eine Exkursion in Bayern. So bleiben mir die letzten Gründe für die verhältnismäßig geringe Teilnahme undeutlich.

Einige Laborforscher, aber auch manche bedeutenden älteren Ornithologen haben vorgeschlagen, künftig auf Exkursionen ganz zu verzichten. Dies hieße aber, scheint mir, das Kind mit dem Bade auszuschütten. Die Namen der letzteren finden sich vielfach in den Exkursionsberichten früherer Kongresse; so scheint deren jetzige Meinung keine grundsätzliche zu sein. Den ersteren mag für ihre besonderen Fragestellungen die Anschauung des oekologischen Gefüges fremder Gebiete entbehrlich scheinen. Den Ornithologen sensu stricto fesselt auch heute noch der Vogel nicht als Objekt, sondern als Problem. Manche Seiten dieses Problems sind ohne Anschauung der spezifischen Umwelt nicht zu begreifen, und zu solcher Anschauung tragen Exkursionen bei.

Die Herren Dr. Peter Berthold (Württemberg-Baden), Prof. Dr. Urs Glutz von Blotzheim (Berner Oberland), Dr. Claus König (Pyrenäen), Dr. Dietrich König (Schleswig-Holstein), Kalevi K. Malmström (Südfinnland), Dr. Alfred Schifferli

(Südalpen), Dr. Seppo Sulkava (Mittel-Finnland) und Dr. Gottfried Vauk (Niedersachsen) haben (die jeweils in Klammern genannten) Exkursionen geplant und vorbereitet, die nicht durchgeführt werden konnten. Ihnen gilt mein Dank nicht nur für ihre Mühe, sondern ebenso für die ausnahmslos klaglose Einsicht in die ökonomischen Gründe für den Ausfall.

Durchgeführt wurden vor dem Kongreß 3 parallele Exkursionen in das Guadalquivir-Delta und die Serrania de Ronda mit insgesamt 38 Teilnehmern, geleitet von den Herren Dr. Javier Castroviejo, Dr. Fernando Alvarez und Pedro Weickert. In das Rhône-Delta fuhren 16 Personen, die Herr Dr. Lucas Hoffmann durch die Camargue und die Crau begleitete. Prof. Dr. Philippe Lebreton und Prof. Dr. Michel Bournaud hatten für 7 Teilnehmer eine Exkursion ausgerichtet, die die Mittlere Rhône vom Teichgebiet Les Dombes bis in die Südausläufer des Schweizer Jura besuchte. Durch die Österreichischen Alpen führte Herr Dr. Gerhard Spitzer 8 Teilnehmer und anschließend 10 Teilnehmer an den Neusiedler See und in den Seewinkel.

Nach dem Kongreß leitete Herr Dr. Spitzer Exkursionen mit 10 Personen in das Donau-Delta und mit 9 Teilnehmern zunächst nach Ungarn und dann ins Donau-Delta. Herr Prof. Walter Wüst zeigte 10 Mitgliedern das nordöstliche Bayern vom Fränkischen Weihergebiet über den Jura bis zum Ries. 15 Personen fuhren unter der Leitung von Herrn Kent Forssgren nach Abisko am Torneträsk in Schwedisch-Lappland. In Finnisch-Lappland besuchten 13 Teilnehmer, geführt von Herrn Olavi Stenman, das Gebiet um Kavigasniemi und den Kevo Nationalpark.

Allen Exkursionsleitern danke ich für Planung, die sorgfältige Durchführung und für die Betreuung der Teilnehmer.

Da ich den Sinn einer jeden Exkursion in dem Zuwachs an Anschauung und Einsicht für den einzelnen Teilnehmer erblicke, scheinen mir Berichte über den Verlauf der Exkursionen an dieser Stelle überflüssig. Nicht überflüssig — um es noch einmal zu sagen — finde ich die Veranstaltung von sorgfältig vorbereiteten und wissenschaftlich gut geleiteten Exkursionen auch auf den künftigen Internationalen Ornithologen-Kongressen.

Sitzungen und Beschlüsse des Permanenten Exekutivkomitees und des Internationalen Ornithologischen Komitees

Am 11. und 12. März 1978 hielt das Permanente Exekutivkomitee eine Sitzung in Frankfurt am Main ab, bei der die Herren Dr. Frith und Phelps nicht anwesend waren. Es billigte die Berichte über die wissenschaftlichen und organisatorischen Vorbereitungen und beauftragte den Generalsekretär mit der Herausgabe der Proceedings und der Beschaffung der dafür nötigen finanziellen Mittel. Der Generalsekretär wurde ferner gebeten, in seinem Bericht ausführlicher als bisher auf die Arbeit des Permanenten Exekutivkomitees (PEC) und des Internationalen Ornithologischen Komitees (IOC) einzugehen. Der vom Präsidenten hergestellte Entwurf einer neuen Satzung für das IOC wurde in einigen Punkten abgeändert und Vorschläge für neue Mitglieder des PEC und IOC sowie für einen Präsidenten des nächsten Kongresses vorbereitet. Überlegungen für den Austragungsort des nächsten Kongresses schlossen sich an.

Eine zweite Sitzung während des Kongresses in Berlin am 5. Juni, bei der alle Mitglieder anwesend waren, beschäftigte sich vorwiegend mit den Modalitäten eines nächsten Kongresses in Moskau. Eine weitere Einladung nach Belgien war soeben eingegangen.

Auf einer dritten Sitzung am 7. Juni wurden die Einzelheiten der Einladung nach Belgien besprochen und beide Einladungen gegeneinander abgewogen. Das PEC sprach sich mit 6 zu 4 Stimmen für die Annahme der Einladung nach Belgien aus. Vorschläge für ca. 50 neue Mitglieder des erweiterten IOC, für den Ersatz der 4 ausscheidenden Mitglieder des PEC und für den Präsidenten des nächsten Kongresses wurden diskutiert.

Das IOC hat in zwei Sitzungen am 6. und 10. Juni eine Reihe wichtiger Entscheidungen getroffen. In der ersten Sitzung, an der 51 Mitglieder teilnahmen, wurde die neue Satzung des Komitees nach einigen redaktionellen Änderungen ohne Gegenstimme angenommen und mit sofortiger Wirkung in Kraft gesetzt. Der Wortlaut ist auf den Seiten 55 bis 62 dieses Bandes abgedruckt. Die neuen Statuten setzen sich aus der eigentlichen Satzung und aus Ausführungsbestimmungen zusammen. Sie ersetzen die Statuten von Rouen 1938, die die letzten 8 Kongresse regiert haben.

Nach der neuen Satzung kann das IOC, bisher auch „Hunderterkomitee" genannt, nun erheblich erweitert werden, denn die Mitglieder, die älter sind als 65 Jahre, werden bei der Begrenzung auf 100 Personen nicht mehr mitgezählt, haben aber volles Stimmrecht. Die Zusammensetzung des Komitees soll die internationale Ausbreitung der Ornithologie widerspiegeln, und die Zahl der Vertreter der einzelnen Länder soll der ornithologischen Aktivität dieser Länder entsprechen. Die Aufgaben des Komitees bestehen in der Wahl des Landes, in dem der nächste Kongreß stattfinden soll; in der Wahl neuer Komitee-Mitglieder, des Präsidenten des nächsten Kongresses, der Mitglieder des PEC; und in der Förderung internationaler Zusammenarbeit.

Das PEC soll nach der neuen Satzung in dem Zeitraum zwischen den Kongressen im Namen des IOC arbeiten und trägt die allgemeine Verantwortung für dessen wissenschaftliche Politik. Es ist bei der Zusammensetzung des jeweiligen Komitees für das Wissenschaftliche Programm anzuhören. Die bisherige bewährte Übung, die Mitglieder des PEC de facto für 8 Jahre arbeiten zu lassen, auf jedem Kongreß nur 4 auszuwechseln, und so die Erfahrungen weiterzureichen, ist nicht in die neue Satzung aufgenommen.

Auf einer zweiten Sitzung des IOC am 10. Juni waren 46 Mitglieder anwesend. Sie wählten einstimmig Prof. Dr. Lars Freiherr von Haartman zum Präsidenten des nächsten Kongresses.

Herr Dr. Devillers überbrachte und erläuterte eine Einladung für den nächsten Kongress nach Belgien, Prof. Dr. Iljitschew nach Moskau. In Belgien würde der Kongreß im August 1982 stattfinden, vermutlich in Brüssel; etwa 250 Teilnehmer könnten im Universitätsgelände untergebracht werden, die übrigen in Hotels. Es werde keine Simultan-Übersetzung geben. Die Herausgabe der Proceedings sei gesichert.

In Moskau würde der Kongreß zwischen Juni und August 1982 stattfinden können. Für die Plenarvorträge werde es eine Simultan-Übersetzung ins Englische geben, für die übrigen Vorträge ausführliche Kurzfassungen in der Sprache der Autoren mit russischer Übersetzung. Die Zahl der Teilnehmer aus der Sowjetunion werde man aus

räumlichen Gründen auf ein Viertel der Gesamtzahl beschränken, für die Teilnehmer aus dem Ausland gäbe es keinerlei Beschränkungen; jeder Ornithologe werde einreisen können, gleichgültig, aus welchem Land er komme. Die Proceedings sollen auf Englisch und Russisch beschränkt werden: pro Vortrag 5 Seiten Englisch und 1 Seite russische Zusammenfassung bzw. umgekehrt.

In der folgenden Abstimmung sprachen sich 19 Mitglieder des IOC für Moskau, 17 für Brüssel aus, 10 enthielten sich der Stimme. Damit war der Kongreß 1982 nach Moskau vergeben.

Nach dieser Entscheidung erklärte der Generalsekretär seinen Rücktritt als Mitglied des PEC: er wolle nicht Mitverantwortung übernehmen für die Durchführung eines Kongresses, bei dem ihm die uneingeschränkte Tätigkeit des PEC und die ungehinderte Teilnahme eines jeden Ornithologen nicht gesichert erscheine.

Das IOC wählte dann 47 neue Mitglieder (die in der Liste auf den Seiten 50—54 dieses Bandes mit einem Stern vor dem Namen gekennzeichnet sind). Es beauftragte das PEC, ein Komitee zu bilden, das rechtzeitig in den nächsten vier Jahren die Zusammensetzung des IOC in Übereinstimmung bringen möge mit der derzeitigen ornithologischen Aktivität der einzelnen Länder.

Es bestätigte die Herren Prof. Glutz von Blotzheim, Prof. Bock, Dr. Frith und Dr. Snow als Mitglieder des PEC und wählte hinzu die Herren Prof. Aschoff, Dr. Brosset, Prof. Iljitschew und Prof. Sick.

Für den Fall, daß der Präsident an seiner Amtsausübung verhindert sein sollte, wurde Prof. Aschoff zum Vertreter gewählt.

Das Standing Committee for the Cooperation of Seabird Research und das International Committee for Bird Ringing wurden zu offiziellen Organen des IOC erklärt mit der Maßgabe, daß ihnen Raum und Zeit für Veranstaltungen auf dem nächsten Kongreß einzuräumen sei.

Decisions of the International Ornithological Committee

The International Ornithological Committee came to some important decisions during two meetings, held on June 6th, 1978, when 51 members were present, and on June 10th with 46 members present. Prof. DONALD S. FARNER presided over both meetings.

1.) The revised Statutes and By-Laws were adopted (printed on pp. 55—60 in this volume).

It was decided that the International Ornithological Committee shall designate a member of the Permanent Executive Committee to act as President in case the latter is incapacitated.

2.) Prof. LARS FREIHERR VON HAARTMAN was elected by acclamation to fill the Presidential Chair of the XVIIIth Congress.

3.) Invitations to host the XVIIIth Congress were offered by the Soviet Union, represented by Prof. ILYICHEV, and by Belgium, represented by Dr. DEVILLERS. It has been decided to hold the XVIIIth International Ornithological Congress in Moskow in 1982.

Due to this decision the Secretary-General retired as a member of the PEC.

Prof. ILYICHEV gave assurance that each foreign ornithologist, coming from whatever country he may, will be allowed to enter the Soviet Union for the Congress and for the excursions. There will be simultaneous translations of the plenary sessions, and there will be a publication of extensive abstracts of the papers in the language of the author with Russian translation. Qualified ornithologists will accompany each excursion. The Proceedings will contain English papers with Russian summaries and Russian papers with English summaries respectively.

4.) The Executive Committee's recommendations for new members of the International Ornithological Committee were adopted after one substitution. The list of members (see below) was approved. The Executive Committee shall nominate a sub-committee for reviewing the composition of the International Ornithological Committee and to bring it in line with present ornithological activities.

5.) The Permanent Executive Committee was reconstituted by the election of Prof. ASCHOFF, Dr. BROSSET, Prof. ILYICHEV and Prof. SICK and by the re-election of Prof. BOCK, Dr. FRITH, Prof. GLUTZ VON BLOTZHEIM and Dr. SNOW.

6.) Prof. ASCHOFF was designated to act as President in case BARON VON HAARTMAN should be incapacitated.

7.) The Standing Committee for the Cooperation of Seabird Research and the International Committee for Bird Ringing were declared official committees of the International Ornithological Committee.

The President 1978—1982

Prof. Dr. Lars Freiherr von Haartman

The Permanent Executive Committee 1978—1982

Prof. Dr. Jürgen Aschoff
Prof. Dr. Walter Bock
Dr. A. Brosset
Dr. Harry J. Frith
Prof. Dr. Urs Glutz von Blotzheim
Prof. Dr. Vladimir Ilyichev
Prof. Dr. Helmut Sick
Dr. David Snow

The International Ornithological Committee 1978—1982

(* = newly elected members)

ARGENTINA

Olrog, C. Chr., Instituto Miguél Lillo, Universidad Nacional de Tucumán, Tucumán

AUSTRALIA

Davies, S. J. J. F., CSIRO, Division of Wildlife Research, Clayton Road, Helena Valley, W.A.
Frith, H. I., CSIRO, Division of Wildlife Research, P.O.Box 84, Lyneham A.C.T.
Rowley, J. C. R., CSIRO, Division of Wildlife Research, Clayton Road, Helena Valley, W. A.
Serventy, D. L., 27 Everett Street, Nedlands, W.A.

AUSTRIA

Bauer, K., Naturhistorisches Museum, Burgring, P.O.Box 417, A-1014 Wien
* Schifter, H., Naturhistorisches Museum, P.O. Box 417, A-1014 Wien

BELGIUM

Devillers, P., Institut Royal des Sciences Naturelles de Belgique, Rue Vautier 31, B-1040 Bruxelles

BRAZIL

Sick, H., Museu Nacional, Quina da Boa Vista, Guanabara ZC.08, Rio de Janeiro

CANADA

* Erskine, A. J., P.O.Box 1327, Sackville, N. B. EOA 3CO
* Falls, J. B., Department of Zoology, University of Toronto, Toronto, Ontario M5S IAI
Gunn, W. W. H., P.O.Box 1229, Spruce Grove, Alberta TOE 2CO
* Keast, A., Department of Biology, Queen's University, Kingston, Ontario K7L 3N6
* Richardson, W. J., LGL Ltd, Environmental Research Ass., 214 Merton Street, Suite 303, Toronto, Ont. M45 1A6

CHILE

Johnson, A. W., c/o Katz Johnson & Co. Ltd., Casilla 327, Santiago

CHINA, P. R.

* Tso-Hsin-Cheng, Institute of Zoology, Academia Sinica, Haiten, Peking(53)

COLOMBIA

* Borreiro, J. I., Dept. de Biologia, Universidad del Valle, Cali

CZECHOSLOVAKIA

* Hudec, K., CSAV, Institute of Vert. Zoology, 60365 Brno, Kvetna 8

DENMARK

* Dyck, J., Institute of Comparative Anatomy, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø
Löppenthin, P., Torvevej 14, DK-2740 Skovlunde
Salomonsen, F., Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen Ø

EIRE

* O'Connor, R. J., Zoology Department, University College of North Wales, Bangor LL57 2UW

FINLAND

Frhr. von Haartman, L., Department of Zoology, University of Helsinki, P. Rautatieck. 13, SF-00100 Helsinki 10

FRANCE

Blondel, J., Station Biologique de la Tour du Valat, 13 Sambuc, B.d.Rh.
Brosset, A., Muséum National d'Histoire Naturelle, Brunoy 91
Dorst, J., Muséum National d'Histoire Naturelle, 55 rue de Buffon, F-75005 Paris 5
Erard, C., C.R.M.M.O., Muséum National d'Histoire Naturelle, 55 rue de Buffon, F-75005 Paris 5
Etchécopar, R. D., C.R.M.M.O., Muséum National d'Histoire Naturelle, 55 rue de Buffon, F-75005 Paris 5
Ferry, C., Faculté de Medecine, F-21000 Dijon
* Frochot, B., Laboratoire d'Ecologie, Université de Dijon, F-21000 Dijon
Jouanin, C., 42 rue Charles Laffitte, F-92200 Neuilly sur Seine
* Mougin, J. L., Museum National d'Histoire Naturelle, 55 rue de Buffon, F-75005 Paris 5
* Thiollay, J. M., 59 rue des Capucines, F-92370 Chaville

FEDERAL REPUBLIC OF GERMANY

Aschoff, J., Max-Planck-Institut f. Verhaltensphysiologie, 8131 Andechs
* Berthold, P., Vogelwarte Radolfzell, Schloß, 7760 Radolfzell 16
Bezzel, E., Gsteigstraße 43, 81 Garmisch-Partenkirchen
Goethe, F., Institut für Vogelforschung, Kirchreihe 19 b, 2940 Wilhelmshaven
* Gwinner, E., Max-Planck-Institut für Verhaltensphysiologie, 8131 Andechs
Immelmann, K., Abteilung für Verhaltensforschung, Universität Bielefeld, Postfach 8640, 48 Bielefeld
Kuhk, R., Schloß Möggingen, 7760 Radolfzell 16
Löhrl, H., Edelweiler 73, 7293 Pfalzgrafenweiler 2
Meise, W., Zoologisches Museum, Papendamm 3, 2 Hamburg 13
* Nicolai, J., Institut für Vogelforschung, An der Vogelwarte 21, 2940 Wilhelmshaven-Rüstersiel
Sauer, E. G. F., Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 162, 53 Bonn 1
Schüz, E., Elmar-Doch-Str. 39, 7140 Ludwigsburg
Zink, G., Vogelwarte Radolfzell, Schloß, 7760 Radolfzell 16

GERMAN DEMOCRATIC REPUBLIC

* Oehme, H., Forschungsstelle für Wirbeltierforschung (im Tierpark Berlin) Am Tierpark 125, DDR-1136 Berlin
* Rutschke, E., Rosenstr. 12, DDR-1502 Potsdam-Babelsberg

HUNGARY

Keve, A., Madártani Intézet, Költö Utca 21, Budapest XII

ICELAND

* Gardarsson, A., Institute of Biology, University of Iceland, Grensasvegur 12, 108 Reykjavik

INDIA

Abdulali, H., 75 Abdul Rehman Street, Bombay 3
Ali, S., 33 Pali Hill Bandra, Bombay 50
Biswas, B., Zoological Survey of India, Indian Museum, Calcutta 700016

INDONESIA

Somadikarta, S., Museum Zoologicum Bogoriense, Bogor, Java

IRAN

* Moravej-Hamadani, H., P.O.Box 1044, Ahwaz

ISRAEL

Zahavi, A., Zoological Institute, University of Tel Aviv, 155 Herzel Street, Tel Aviv

ITALY

Frugis, S., Italian Center of Ornithological Studies, Zool. Institute, Parma
Moltoni, E., Museo Civico di Storia Naturale di Milano, Corso Venezia 55, Milano

JAPAN

* Morioka, H., Dept. of Zoology, National Science Museum, Hyakunin-Cho 3-23-1, Shinjuku-ku, Tokyo 160
* Nakamura, T., Department of Biology, Yamanashi University, Kofu 400
Yamashina, Y., Yamashina Institute for Ornithology, 8-14 Nampeidai-machi, Shibuya-ku, Tokyo
* Yoshii, M., Bird Migration Research Center, Yamashina Institute for Ornithology, 8-20 Nampeidai-machi, Shibuya-ku, Tokyo 150

JUGOSLAVIA

* Matvejev, S., ul. Milcinskega 14, 6100 Ljubljana

KENYA

Forbes-Watson, A. D., c/o Animal Ecology Research Group, Dept. of Zoology, University of Oxford, South Parks Rd., Oxford, United Kingdom

MEXICO

Phillips, A. R., Apartado Postal 370, San Nicolas de Garza, Nuevo Leon

THE NETHERLANDS

* Drent, R. H., Zoölogisch Laboratorium, University of Groningen, Kerklaan 30, Haren (Gron.)
Mees, G. F., Rijksmuseum van Natuurlijke Historie, P.O.Box 9517, 2300 RA Leiden
Perdeck, A. C., Institut voor Oecologisch Onderzoek, Vogeltrekstation, Kemperbergerweg 11, Arnhem
Voous, K. H., Maasdamlaan 28, Huizen N.H.

NEW ZEALAND

Falla, R. A., 41 Katari Road, Days Bay, Eastbourne
Kinsky, F. C., c/o National Museum, Private Bag, Wellington
* Westerskov, K. E., Department of Zoology, University of Otago, Dunedin

NORWAY

Holgersen, H., Stavanger Museum, N-4000 Stavanger
* Haftorn, S., Zoologisk Avdeling, DKNVS, Muséet, Erling Skakkes gt. 47 b, 7000 Trondheim

PERU

Koepcke, H. W., Zoologisches Institut u. Zool. Museum der Universität Hamburg, Papendamm 3, D-2 Hamburg 13, Bundesrepublik Deutschland

PHILIPPINES

Rabor, D. S., Museum of Natural Science, Mindanao State University, Marawi City

POLAND

Tomiałojc, L., Museum of Natural History, Wrocław University, U. Sienkiewicza 21, 50-335 Wrocław

RUMANIA

* Vasiliu, D. G., Aleea Teilor, Bloc 2 C, sc. B I/4, 0300 Pitesti, 1

SENEGAL

Dupuy, A., Parcs Nationaux du Senegal, B.P. 37, Tambacounda

SOUTH AFRICA

Liversidge, R., McGregor Museum, Box 316, Kimberley 8300
Siegfried, W. R., Percy Fitzpatrick Institute for African Ornithology, University of Cape Town, Rondebosch
Winterbottom, J. M., 9 Alexandra Avenue, Oranjezicht, Cape Town 8001

SOUTH KOREA

* Won, Pyong-Oh, Ornithology Institute, Department of Biology, Kyung Hee University, Seoul

SPAIN

* Castroviejo, J., Estación Biológica de Doñana, Paraguay 1, Sevilla
* Herrera, C. M., Virgen de la Presentacion 2, Sevilla 1

SWEDEN

Curry-Lindahl, K., Ministry of Foreign Affairs, Box 16121, 10323 Stockholm 16
* Enemar, A, Zoological Institute, University of Gothenburg, Gothenburg
* Svensson, S. E., Ecology Building, Helgonavägen 5, S-22362 Lund

SWITZERLAND

* Bruderer, B., Schweizerische Vogelwarte, CH-6204 Sempach
Géroudet, P., 37 Avenue de Champel, CH-1206 Genève
ıGlutz von Blotzheim, U., „Eichhölzli", CH-6204 Sempach
Schifferli, A., Wygart, CH-6204 Sempach
Sutter, E., Naturhistorisches Museum, Augustinergasse 2, CH-4051 Basel

UNITED KINGDOM

* Burton, P. T. K., British Museum (Natural History), Park Street, Tring, Herts. HP23 6AP
Cramp, S., 32 Queen Court, London WC1N 3BB
* Fry, C. H., Aberdeen University, Zoology Department, Tillydrone Avenue, Aberdeen AB9 2TN
Matthews, G. V. T., The Wildfowl Trust, Slimbridge, Gloucestershire
Mountfort, G., Plovers Meadow, Blackboys, Sussex
* Newton, I., 12 Hope Terrace, Edinburgh EH9 2AS, Scotland
Nicholson, E. M., 13 Upper Cheyn Row, London SW3 5JW
Olney, P. J. S., Zoological Society of London, Regent's Park, London NW1 4RY
* Perrins, C. M., Edward Grey Institute, Department of Zoology, South Parks Road, Oxford

Snow, D. W., British Museum (Natural History), Tring, Herts. HP23 6AP
Tinbergen, N., Animal Behaviour Research Group, Department of Zoology, University of Oxford, Parks Road, Oxford

U. S. A.

Bartholomew, G. A., Department of Zoology, University of California, Los Angeles, Calif. 90024
Bock, W. J., Department of Biological Sciences, Columbia University, New York, N.Y. 10027
Eisenmann, E., American Museum of Natural History, 79th Street and Central Park West, New York, N.Y. 10024
Farner, D. S., Department of Zoology, University of Washington, Seattle, Wash. 98105
* Gill, F.B., Academy of Natural Sciences, 19th Street and Parkway, Philadelphia, PA 19103
* Howell, Th., Department of Biology, University of California, Los Angeles, Calif. 90024
* King, J. R., Department of Zoology, Wahington State University, Pullman, Wash. 99164
* Marler, P., Rockefeller University Field Research Center, Tyrrel Road, Millbrook, N.Y. 12545
Mayr, E., Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138
Peterson, R. T., 125 Neck Road, Old Lyme, Conn. 06371
Ripley, S. D., Smithsonian Institution, Washington D.C. 20560
* Short, L. L., American Museum of Natural History, 79th Street and Central Park West, New York, N.Y. 10024
Sibley, C. G., Peabody Museum of Natural History, Yale University, New Haven, Conn. 06520
Storer, R.W., Museum of Zoology, University of Michigan, Ann Arbor, Mich. 48104
Traylor, M., Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Ill. 60605
Wetmore, A., Smithsonian Institution, Washington D.C. 20560
* Woolfenden, G. E., Department of Biology, University of South Florida, Tampa, Fl. 33620

U.S.S.R.

* Dolnik, V. R., Zoological Institute Leningrad and Biological Research Station (Rybatchy), Leningrad
* Flint, W. E., Central Laboratory for Nature Conservation, Znamenskoye-Sadki, 142790. P.O. Vilar, Moscow Region
Ilyichev, V. D., Ringing Center, Fersman Street 13, 117312 Moscow
Isakov, Y. A., Institute of Geography, Academy of Sciences of U.S.S.R., Staromonetny 29, Moscow
Kumari, E., Zoological Institute, Academy of Sciences of the Estonian S.S.R., Vanemuise 21, Tartu, Estonian S.S.R.
* Kurochkin, E. N., Paleontological Museum of the USSR Academy of Sciences, Leninsky Prospekt 16, Moscow 117071

VENEZUELA

Phelps, W. H., Colección Ornitológica Phelps, Apartado 2009, Caracas 101

ZAIRE

De Bont, A. F., Walenpotstraat 1 A, B-3060 Bertem, Belgium

ZAMBIA

Dowsett, R.J., Nyiko National Park, Private Bog Chilinda, PO Rumphi, Malawi

The International Ornithological Committee

STATUTES

Article I

Objectives and Purposes

The International Ornithological Committee (IOC) (1) promotes international collaboration and cooperation in ornithology and (2) as it deems desirable and useful, it encourages international collaboration and cooperation between ornithology and other biological sciences.

To effect these objectives and purposes the IOC sponsors and promotes the International Ornithological Congresses; establishes and sponsors commissions and committees as it deems appropriate and desirable; establishes or sponsors other international ornithological activities as it deems appropriate; and functions as the Section of Ornithology in the International Union of Biological Sciences.

Article II

Membership and Functions

1. Size. The size of the membership of the IOC is determined by the Committee, but not to exceed the number specified in the By-Laws (Art. I).

2. Representation. The membership shall be representative of the international distribution of ornithologists, and the number of members from each country shall be proportional to its ornithological activity.

3. Election. New members are elected by the IOC at a regular meeting at the International Ornithological Congress from a list of nominations prepared and presented by the Permanent Executive Committee. Additional nominations may be made by any member at the time of the meeting. If seconded, such nominations are added to the list presented by the Permanent Executive Committee. Election to the Committee requires a simple majority vote of the members present and voting.

4. Term. The term of membership is indefinite unless the member resigns voluntarily or is absent from regular meetings of the IOC at two consecutive Congresses which constitutes automatic resignation. Resigned members may be re-elected.

5. Meetings. The IOC meets at least twice during each International Ornithological Congress. The quorum for transaction of business at a regular meeting consists of the members present at the meeting. A member must be in attendance at a meeting in order to cast his vote.

6. Duties. The duties of the IOC are (a) to select the site of the next Congress; (b) to elect new members; (c) to elect the President of the next Congress; (d) to elect members of the Permanent Executive Committee; and (e) to take actions appropriate and necessary to carry out its stated objectives and functions (Art. I).

7. Special meetings. The President, under extraordinary circumstances, may call a special meeting of the IOC. He is obligated to do so on receipt of a petition signed by one-quarter of the members. The date set for a special meeting must permit reasonable

time for consideration of the agenda and for travel arrangements. A quorum for a special meeting is one-third of the members of the IOC. Failure to attend a special meeting shall not count toward automatic resignation (Art. II: 4).

8. Presiding officer. The President presides at the meetings of the IOC.

9. Communications. Actions of the IOC are communicated to the Congress and published either in the Proceedings of the Congress or in some other publication, as approved by the Permanent Executive Committee.

Article III

Officers

A. The President

1. Election. The President is elected by a simple majority vote of the members present and voting at a regular meeting of the IOC at the International Ornithological Congress. He is not eligible for election to the same office in two successive congresses.

2. Succession. After election of the President and of the PEC, the IOC will designate, by election, one of the members of the PEC to serve as President in case of the inability of the elected President to continue in his office.

3. Term. The President holds office from the conclusion of the Congress at which he is elected until the conclusion of the following congress.

4. Duties. The President of the IOC also serves as chairman of its Permanent Executive Committee (PEC), as President of the International Ornithological Congress, and (or designates a representative) as a member of the Board of the Division of Zoology of the International Union of Biological Sciences. He presides at meetings of the IOC, of its Permanent Executive Committee and of the International Ornithological Congress, and appoints committees and commissions (with the exception of the IOC and the PEC) of the IOC and of the Congress. After consultation with the host organization of the forthcoming congress, the President shall appoint the Secretary-General.

5. Membership in the IOC. Past Presidents are permanent members of the IOC.

B. The Secretary-General

The Secretary-General serves as Secretary-General and Treasurer of the Congress, as Secretary and Treasurer of the International Ornithological Committee, as Secretary of its Permanent Executive Committee and as Secretary of the Section of Ornithology of the International Union of Biological Sciences. He has the over-all responsibility for all local and financial arrangements for the International Ornithological Congress for which he has been appointed. He serves until the Secretary-General of the following International Ornithological Congress is designated. He serves ex-officio as a member of the Permanent Executive Committee until the end of the following Congress.

Article IV

The Permanent Executive Committee (PEC)

1. Membership.

a. The President of the International Ornithological Committee (IOC) as in Art. III: A, 4.

b. An even number of elected members, as specified by the By-Laws. No more than one of these members may be from a single country. These members shall be elected with proper attention to an adequate international distribution in the Permanent Executive Committee.

c. The Secretary-General is an ex-officio member of the PEC until the end of the following Congress as in Art. III: B.

2. Election. Nomination and election of members of the PEC shall follow election of the President. Nomination shall be proposed by the existing PEC. Any member of the IOC present at the meeting may make nominations. If seconded these are added to the nominations proposed by the PEC. Election of members of the PEC is by simple majority vote of the members of the IOC present and voting. Elected members are eligible for re-election as an elected member of the PEC for one additional term.

3. Term. The PEC shall serve from the conclusion of the Congress at which it is elected to the conclusion of the following Congress.

4. Duties.

a. During the Inter-Congress period, the PEC acts on behalf of the IOC.

b. During the Inter-Congress period, the PEC has general responsibility for the scientific policy of the IOC including the program of the Congress, as specified in the By-Laws (Art. IV: 4).

c. At a meeting of the IOC at the International Ornithological Congress, it provides:

(1) Nominations for the office of President, for the elected members of the PEC, and for the designated presidential successor (Art. III: A, 2);

(2) A recommendation concerning the host country and organization for the ensuing congress after due consideration of all invitations;

(3) Nominations for new members of the IOC with due consideration of Art. II: 2;

(4) Recommendations for re-election of members considered to have resigned because of absence from two consecutive meetings, as specified in Art. II: 4;

(5) Advice and counsel concerning any other matters deemed to be of interest, within the purvue, or among the responsibilities of the IOC.

Article V

Amendment of the Statutes

1. Proposal of amendment. Proposals to amend the statutes require the signatures of at least five members of the IOC from at least three countries, and must be transmitted to the Secretary-General at least twelve months before the next International Ornithological Congress. The Secretary-General will distribute the proposed amendments to all members of the IOC at least four month prior to the Congress. At the meeting of the IOC at the Congress the PEC will present its recommendation on each proposed amendment.

2. Adoption. Adoption of an amendment by the IOC requires two-thirds majority vote of the members present and voting. Adopted amendments become effective at the close of the Congress.

Article VI

Enabling Clause

Adoption of these statutes requires a two-thirds majority vote of the members of the existing IOC present and voting at a regular meeting of the IOC at the International Ornithological Congress at which they are presented, having been distributed to the members prior to that meeting. Adoption of these statutes shall replace the Règlement des Congrès Ornithologiques Internationaux adopted in Rouen in 1938 and all amendments passed thereafter. If adopted, these statutes become effective immediately.

BY-LAWS

Article I

The size of the International Ornithological Committee (IOC)

The membership of the Committee be not more than 100. Members over 65 years of age and Past Presidents are not counted in this limit.

Article II

Meetings of the International Ornithological Committee

1. Sufficiently prior to the regular meeting of the IOC at the International Ornithological Congress the Secretary-General shall distribute to all members an agenda of the meeting.
2. Members are requested to inform the Secretary-General of their intention to attend the meeting, and/or to resign from the Committee.
3. An agenda and information on matters to be covered shall be sent to members with the notice of any special meeting called by the President.

Article III

Membership of the Permanent Executive Committee (PEC)

In addition to the officers specified in Art. IV of the Statutes, the International Ornithological Committee elects eight members in accordance with Art. IV: 1, b of the Statutes.

Article IV

The International Ornithological Congresses

1. The frequency of the Congress. Congresses will be held at four-year intervals unless, for compelling reasons, the IOC, or the PEC acting on its behalf, deems otherwise.

2. The site and time of the Congress. After consultation with the PEC and the host organization, and due consideration of the interests and convenience of the members, the site in the host country and time of the Congress are fixed by the Secretary-General.

3. Membership of the Congress. Membership in an International Ornithological Congress shall be open to all ornithologists and students of avian biology without distinction as to country of origin upon payment of the stated congress fee, if any. Membership and attendance at a Congress shall be in accordance with the general policies of the IUBS. Any limitation on the number of active members of the congress may be made by the Secretary-General only after consultation with and agreement by the PEC. Such limitation must be clearly stated in Congress announcements. In the case of limitation in the number of active members, provision must be made for associate members which may not be limited in number. Members of the IOC may not be denied a place as an active member upon payment of the congress fee.

4. The Scientific Program of the Congress. After consultation with the PEC and the host organization the President appoints the Scientific Program Committee. This Committee consists of three or more members from the host country and members from at least three other countries. The Secretary-General is a member ex-officio of the Scientific Program Committee. This committee is responsible to PEC for the scientific program of the Congress.

5. The organization of the Congress. The general organization of, and the arrangements for, the Congress are the responsibilities of the Secretary-General.

6. The Proceedings of the Congress. The Secretary-General is responsible for the publication of the Proceedings of the Congress. If he does not serve as editor of the Proceedings, he appoints the editor after obtaining concurrence from the President.

7. Finances of the Congress. The Secretary-General is the treasurer and principal finance officer of the Congress and as such is responsible for all financial matters of the Congress. In consultation with the President he develops the budget and fixes the Congress fee. After all fiscal obligations have been absolved, any surplus funds, including any from the Proceedings, are made available for Inter-Congress activities, including arrangements for the ensuing Congress.

Article V

Amendment of the By-Laws

1. Proposal of amendment. Proposals to amend the By-Laws require the signature of at least three members from at least three countries and must be transmitted to the Secretary-General at least twelve months in advance of the next International Ornithological Congress. The Secretary-General will distribute at least four month prior to the Congress the proposed amendments to the members of the International Ornithological Committee. At the meeting of the IOC at the Congress, the PEC will present its recommendation on each proposed amendment.

2. Adoption. Adoption of proposed amendments to the By-Laws by the IOC requires a simple majority vote of the members present and voting. Adopted amendments become effective at the close of the Congress.

3. Conflict with the Statutes. No amendment of the By-Laws can have the effect of modification of the Statutes.

Article VI

Enabling Clause

Adoption of these By-Laws requires prior adoption of the proposed statutes, and requires a simple majority vote of the members of the existing Committee present and voting at a regular meeting of the IOC at the Congress at which they are presented, having been distributed to the members prior to that meeting. Adoption of these By-Laws shall replace any existing By-Laws and regulations (formal and informal) of the IOC and of the International Ornithological Congresses. If adopted, these By-Laws become effective immediately.

The International Ornithological Committee (IOC), the so-called Committee of 100 and the International Ornithological Congresses operated under the Règlement adopted at the Rouen (IX) Congress in 1938 (see Proceedings IXth Congress, pp. 661—662) and subsequent modifications. The decision was reached at the Hague (XV) Congress to revise these rules (see Proceedings XVth Congress, p. 12). Unfortunately no action was taken prior to the Canberra (XVI) Congress. President Donald S. Farner assumed the task of drafting Statutes and By-Laws which were circulated to members of the PEC, recent past-presidents and secretaries-general. A revised draft was discussed and further revised at the meeting of the PEC in Frankfurt a. M., March 1978. This draft was submitted to all members of the IOC prior to the Berlin (XVII) Congress. It was discussed, amended slightly and adopted at the first meeting (6 June 1978) of the IOC at the Berlin Congress. The new Statutes and By-Laws became effective immediately and governed the actions taken at the second meeting of the IOC. Final wording of the Statutes and By-Laws was checked by an Editorial Committee appointed by President Farner, consisting of W. J. Bock (Chairman), H. J. Frith, and K. H. Voous.

Report of the Standing Committee on Ornithological Nomenclature

Dr. Eugene Eisenmann (USA), Chairman of the Standing Committee on Ornithological Nomenclature, submitted the following report.

The Standing Committee on Ornithological Nomenclature of the International Ornithological Congresses is an international body appointed by the president of the Congress. It serves until the close of that Congress. Its functions are advisory on matters of avian nomenclature. Members of the Committee are consulted on nomenclatural questions by ornithologists; recommendations are made by the committee on ornithological matters that come before the International Commission on Zoological Nomenclature and sometimes on proposals for changes in the Code of Nomenclature that may have special impact on bird names; and occasionally the Committee offers recommendations on avian nomenclature to ornithologists. Usually a public session on nomenclature is held during the International Ornithological Congress at which the chairman of the Committee reports on the actions of the groups, solicits comments and recommendations and presides on discussions of nomenclatural problems of general interests. Meetings of the Committee may also be held.

No meeting of the Standing Committee was held at the XVI International Ornithological Congress, Canberra, Australia and no report of the Committee was published in the proceedings. President Donald S. Farner of the XVII Congress appointed the following as members of the Standing Committee on Ornithological Nomenclature for that Congress: Eugene Eisenmann (USA), Chairman; Pierre Devillers (Belgium); Jean Dorst (France); David Snow (United Kingdom); Finn Salomonsen (Denmark); Karel Voous (Netherlands); George Watson (USA).

A public session of the Committee was held in the evening of 9 June during the Berlin Ornithological Congress. The chairman, Dr. E. Eisenmann, reported on the activities of the Committee which included several written recommendations to the International Commission on applications involving avian scientific names, and help or participation in applications to the Commission. In all cases of ornithological names on which the International Commission had acted, the recommendations of the Committee had been accepted. The chief problem is that the International Commission takes a long time before an application is brought to a vote and the decision is published. To some extent this difficulty is reduced by provisions in the Code that after an application is filed with the Commission and notice of the application is published by the Commission, zoologists are supposed to follow prevailing, that is to say, majority, usage until a decision is reached and published. Deferring to the wishes of invertebrate zoologists and contrary to those of ornithologists and many other vertebrate zoologists, the provisions in the code for automatic action of the 50-year stature of limitations invalidating unused senior synonyms was repealed and replaced by provisions requiring formal application and action by the Commission to invalidate such names.

The problem of family-group names, which under the Code are now subject to the rule of priority although there is provision by which the International Commission may validate usage, is a very troublesome one in ornithology. Family-group names are those for tribes, subfamilies, families and superfamilies; names for suborders, orders and superorders are not included in this provision and are not subject to the rule of priority.

The problem is that most family-group names that have been long and consistently used in avian classification may not be the oldest name and adequate published synonymies of avian family-group names are lacking. The Secretariat of the Commission has taken the position that to invalidate senior family-group names requires exercise of Plenary Powers of the Commission, and that validation of the generally used family-group name would not give it precedence over an earlier name unless that name had been expressly mentioned in the application. This means that in order to validate effectively currently used family-group names, a check of the synonymy for each name is required which entails an extensive and burdensome bibliographic research. Otherwise a second application will have to be made if an earlier competitive name is brought to light.

At the public session during the Berlin Congress, the question of an "official" list of bird names was raised. It was pointed out that scientific names depend not merely on nomenclatural rules and decisions, but even more on varying and changing opinions as to taxonomic relationships. The Standing Committee on Ornithological Nomenclature has not, and should not have, any jurisdiction over matters of taxonomy. Moreover, most avian systematists consider any attempt to freeze taxonomic opinion into an official world list of birds to be undesirable—as was evident from the full discussion at the XIV Ornithological Congress, Oxford 1966 (see pp. 365—367 of those Proceedings). There was a consensus that at the species level there exists a carefully prepared "Reference List of Birds of the World" by MORONY, BOCK & FARRAND (1975) published by the American Museum of Natural History which, although in no sense official and although it admittedly contained some errors and was being revised, could conveniently be used by those ornithologists requiring a list of avian species but unable to undertake their own taxonomic studies.

Report of the Standing Committee for the Coordination of Seabird Research

A Standing Committee was set up at the XIV International Ornithological Congress in 1966 to improve liaison in research on seabirds, and has regularly organised a discussion at the Congresses since then, summarised in the Proceedings of the XV and XVI Congresses (p. 15—18 and 7—11 respectively). Another meeting was convened at the XVII Congress on the morning of 7 June and subsequently adjourned until the afternoon of 9 June. Professor K. H. Voous took the chair, and 31 people from twelve countries participated.

The Chairman welcomed the participants and explained that the main function of the Committee so far had proved to be the organisation of this open meeting, which provided a forum for the members of the growing number of regional Seabird Groups in the world, now located in Europe, the (northern) Pacific, South Africa and Australasia, to consult together. On this occasion it proposed that the discussion should include the position of the Committee and the Seabird Groups; their publications; techniques of investigation of the biology of the birds, especially at sea, breeding censuses, and mortality, notably that due to toxic chemicals and disease. There were also proposals for regional censuses of European breeding seabirds and wintering gulls.

In the first place it was noted that while there had been a proposal for a plenary session devoted to seabirds at this Congress, the Committee had not been consulted and it had been allowed to lapse. Mr. Stanley Cramp described this as a tragedy, and proposed that the Committee should offer to organise one in future. This was agreed unanimously. It was noted that alternatively two members of the Committee who were unable to attend, Dr. Kees Vermeer of Canada and Dr. Jerry van Tets of Australia, had written apologising and suggesting in the first case that it might be better to organise an independant International Marine Bird Congress, and in the second that a more cosmopolitan approach should be adopted than was originally suggested for the plenary session devoted to the North Atlantic proposed for this Congress. Dr. Vermeer offered to organise a first meeting in Victoria, British Columbia, in 1982. It was considered that this was a matter for consideration by the regional Seabird Groups.

Dr. John Croxall of the British Antarctic Survey also reported that the Bird Biology Subcommittee of the Scientific Committee for Antarctic Research (S.C.A.R.) had also recently met at the Committee's fifteenth international meeting in France to discuss a number of research proposals, including the general use of a card for recording birds at sea derived from that used by the Australians for eight years, and plans for colour-banding, research on *Larus dominicanus* in South America, and the use of satellites for tracking, for development during the multinational biomass research programme for the next decade. Its objectives would include an estimate of the biomass of Antarctic seabirds and the selection of species for monitoring. It was notable that in the first case Antarctic birds (90 % penguins) equal the current whale stocks and half the seal stocks in biomass, and a joint two-year survey is required to give a better understanding of their stock-levels, population dynamics, and especially the non-breeding population. In the second case certain species and localities require more detailed study, especially to detect changes in their marine prey stocks. S.C.A.R. should be establishing an interim committee to review sites and species within the next year, which would require funds.

The Chairman proposed that the Secretary should be informed of all similar developments. Prof. G. M. Winterbottom added that the Cape Bird Club proposed to hold a symposium on seabirds in South Africa in 1979, and the Secretary remarked that the (North American) Colonial Waterbird Group would be holding one in the autumn of 1978 as well. Dr. Gavin Johnston remarked that the Australasian Seabird Group was also organising a meeting for the Royal Australasian Ornithologists' Union on Norfolk Island. Dr. Ralph Schreiber said that the Pacific Seabird Group had already held three annual meetings of 200 people and proposed to have another in California in January. Dr. George Watson remarked that there was a need to circulate news of such events, including the activities of the Colonial Waterbird Group, which had begun to take an interest in the behaviour of birds at sea off eastern North America. The Secretary remarked that each group already had a newsletter which reported the activities of the others, and that the original British group which has some funds derived from royalties for the book reporting its national census also intermittently produces a printed report.

Dr. Schreiber remarked that many of the activities of members of the Pacific Group had depended upon United States government finance, and were now running into economic difficulties. The Secretary reported that the British group had similar difficulties, made worse by a shortage of people prepared to undertake the administration. Dr. Watson remarked that there was room for more rationalisation, for example by combining the Pacific and Colonial Waterbird Groups in North America, though their members failed to agree. Dr. Finn Salomonsen commented that it might be useful if the North Americans would also interest themselves in Greenland, but Dr. Watson said that the American Ornithologists' Union specifically excludes Greenland from their sphere of interest. The Secretary remarked that there is a great need for more work in Iceland and Spitsbergen as well, not to mention the Mediterranean, before we begin to consider remoter areas. There is a need to organise more distant exploration.

It was agreed that there was a need to coordinate policy over publications, including news of meetings, research programmes and funds, and abstracts of talks and publications. Several periodicals such as the Auk would be prepared to take abstracts, and indeed the Emu now also deals with Australasian regional ones. Dr. John Coulson observed that marine mammalogists also have similar problems and their own information service. Dr. Watson was requested to confer with the Chairman and Secretary and report back to the Standing Committee with a policy for publications.

It was noted that a growing number of regional groups are now studying birds at sea, on both sides of the North Atlantic, in the eastern North Pacific, and different parts of the Southern Ocean. Dr. Watson remarked that recording methods became exhausting when every bird had to be recorded and processed manually, while computors are expensive. The original U.S. Pacific Program had lapsed when funds were withdrawn, but Moncton University and subsequently the Wildlife Service had subsequently secured them in Canada. There was a need to standardise techniques. Dr. Coulson observed that not only the methods but their use in different situations and the way in which the results are reported need standardising as well. Sir Hugh Elliott said that it is necessary that people should always record their methods. The Secretary said that he regretted that this was not included in the report of the British national breeding census, but that he had since been collecting figures for the whole of northwestern Europe and would place them on record when reporting the results.

It was remarked that in addition to breeding censuses there is a particular need to assess and standardise methods used for surveys of mortality. In Europe they are now usually expressed in terms of birds per kilometre and the percentage oiled, and comparable figures are needed for other parts of the world. Dr. WATSON observed that there is a need for more repeat surveys to assess how many bodies are really coming ashore. Dr. JOHN WARHAM remarked that the more detailed surveys tend to be self-limiting because nobody wishes to deal with large numbers of decaying bodies. Their investigation tends to present difficult pathological problems as well; in addition to pollution, considered later, they may also die naturally in a variety of ways, as a result of the weather, or poisoning by various micro-organisms such as dinoflagellates at sea and botulism inland, or epizootic disease. Dr. C. M. PERRINS reported that there is now a virologist working on seabirds at the Edward Grey Institute and appealed for material, especially relating to puffinosis; he can supply details.

The meeting on Friday afternoon, which was chaired by Dr. GEORGE WATSON, began with a special discussion of observations at sea. The Secretary pointed out that the basic techniques were defined by POUL JESPERSON in the 1920s, and that a vast mass of uncritical notes have been amassed since the 1950s by the Royal Naval Bird-watching Society which unfortunately while of some distributional interest defy quantitative analysis; and the Society now appears to be giving up any attempt to record them methodically. Dr. WATSON reported that the Smithsonian Institution workers recorded the number of birds seen per nautical mile and multiplied this by a factor for the visibility to obtain densities, though he had doubts about the distance to which different species can be seen. It was reported that the Outer Continental Shelf Environmental Assessment Program which is conducting lavish emergency surveys in Alaska is determining the distance with range-finders, but is was postulated that only radar might prove reliable. The Secretary said that the British scheme merely recorded birds detected with the naked eye, as this was less fatiguing and they could all normally be identified with binoculars if necessary. Dr. PIERRE DEVILLERS remarked that there are many other factors besides the visibility that need to be considered, such as the speed of the bird relative to the boat, the state of the sea, and whether the birds are uniformly distributed or gathered in flocks.

On further discussion Dr. WATSON agreed that possibly the most useful basic recording unit is a short period of time such as ten minutes, which is used on opposite sides of the North Atlantic by first the Canadians and then the British. This is short enough to allow a good deal of flexibility over observation periods while providing a sensitive indication of local variations in distribution, and can easily be combined to give larger units. It was noted however that in Alaska a period of fifteen minutes is being used instead, which does not facilitate easy conversions and comparisons. Difficulties are also encountered in dealing with birds dispersed in different ways, for example uniformly, in flocks, or following in the wake. It was considered that space should be allowed on recording cards to indicate the different types of observation, which may have to be analysed separately. It was considered desirable to establish a subcommittee to consider recording techniques.

When the full meeting was reconvened it returned to the consideration of the need for surveys of breeding birds. A number in north-west Europe have led to increasing emphasis on the need for better census techniques, and Dr. JOHN WARHAM said that

even worse problems are encountered where there are more burrowing species which nest together in Australasia. Dr. JOHN COULSON observed that once a crude baseline is established there is usually a need to answer specific questions; for example with the Black-legged Kittiwake which interests him there is now increasing evidence for adult mortality leading to local declines complicating the sustained general increase. The secretary observed that current policy in Britain is to carry out general surveys at long intervals, keeping a check on the situation between them with sample censuses, and investigating specific problems as they arise. Dr. CROXALL said that S.C.A.R. is pursuing the same policy in the Southern Ocean, and Dr. DEVILLERS that only special surveys are possible in South America, where it would be particularly worth-while to pay more attention to Patagonia. Sir HUGH ELLIOTT observed that there is also a need for further surveys of the Tristan da Cunha group, where the number of *Puffinus gravis* on Nightingale Island has apparently doubled from two to four million, but the first oil pollution has been reported. Dr. CHRIS FEARE reported that there are other problems in the Indian Ocean, where pollution is not evident yet, but the boobies in particular are being killed by man and the numbers of species which breed throughout the year are particularly hard to assess. Dr. DEVILLERS enquired about the Pacific, and Dr. WARREN KING said that as far as is known there are only occasional specific threats at the moment; the Secretary observed that there is a particular need for more news from the western North Pacific from New Guinea north-west to China. It was observed that there are intermittent wrecks of migrating shearwaters in Japan, where more is now being learnt about bird movements from a banding programme.

Dr. KING then commented on some other places requiring attention, such as the coast of Venezuela, and Dr. BOURNE added the Gulf of Guinea and Bay of Bengal, remarking that there are also political difficulties in such areas. Dr. DEVILLERS pointed out that the guano birds of Peru are also reduced by 90 %, and casual investigations from the north are insufficient. It was concluded the most important subjects for concern at the moment are the situation in western South America and where birds are being caught in nylon nets in the Arctic. Dr. CLAUDE JOIRIS remarked that it is a pity that there are so few opportunities for investigation, but was assured that there are now research vessels of a number of nations available. Dr. KING reported that U.S. observers are now also accompanying the Japanes fishing vessels reported to be killing half a million birds a year in the North Pacific.

Dr. SCHREIBER observed that human visits to breeding stations are becoming an increasing problem. Whole colonies of pelicans and Heermans Gulls *Larus heermanni* have been wiped out in the Sea of Cortez. There is a need to control tourism. Dr. BOURNE observed that if the movements of tourists are regulated the birds often become adapted to their presence. Dr. WATSON commented on the particular problem presented for the Least Tern *Sterna albifrons* by recreational activities on its breeding beaches all round the western world. In the eastern USA it is starting to nest on roof-tops. Dr. JAN WATTEL said that if we wish to retain seabird colonies in populated areas this is only possible if they have wardens.

Further problems are presented by introduced mammals. The Secretary said he had spent a good deal of the previous winter on a campaign to prevent the establishment of a mink farm in the Orkneys next to the second-largest seabird colony in Britain. Dr. FEARE remarked on the problems presented by rats in the Seychelles, and Dr. WATTEL

on the attempts being made to remove introductions from the Galapagos, though Dr. DEVILLERS said that there had been local administrative difficulties. Sir HUGH ELLIOTT remarked how goats had been removed from Tristan da Cunha and reduced to two of the same sex on Round Island, Mauritius, by shooting. Dr. WARHAM said that even rabbits which survive on Round Island had been eliminated from an island off southern New Zealand, but the birds now suffered from another introduction, becoming hooked on African Boxthorn. On Macquarie Island the introduced cats, rabbits and rats presented a complex problem because they interact on each other; the cats possibly do most damage but the rabbits and rats may be hardest to eliminate. It was resolved that there is an urgent need for much more research in different parts of the world to find ways to eliminate introductions.

There was a discussion of the damage caused by 200,000 tons of crude oil from the wreck of the Amoco Cadiz in northern France the previous spring. It was a comparatively light, toxic oil and most of the birds and other marine life which encountered it had died rapidly. It was carried high on the shore by the spring tides, and penetrated it for several metres, though the superficial deposits had now been washed away. It had killed a number of birds banded in Britain, but arrived five weeks earlier than the oil from the Torrey Canyon in 1967 and had less effect on the breeding population. The Puffins *Fratercula arctica* on the Sept Iles sanctuary which were reduced from 2000 to 500 pairs then and had increased to 800 pairs were down to 400 pairs again, and the Razorbills *Alca torda* to 30 pairs. Dr. COULSON observed that we need to know more about the ability of birds to respond to such impacts, especially the non-breeding population. Dr. F. GOETHE reported that birds are also sometimes vulnerable outside the breeding season, for example where most north European Shelduck *Tadorna tadorna* moult on the Knechtsand in the late summer, and where a large part of the sea-duck population winter in the Baltic.

No new problems had been noticed with toxic chemicals. Following the control of DDT discharges the Brown Pelicans *Pelecanus occidentalis* are now laying eggs with thicker shells in California. The Sandwich and Little Terns *Sterna sandvicensis* and *S. albifrons* are beginning to recover in Holland, where there have also been problems with effluents, though the former are still only a fifth of their former numbers. The Cormorants *Phalacrocorax carbo* have increased from 1200 to 2000, but the number of Eiders *Somateria mollissima* remains the same. It was reported that little trouble from pollution has been noticed in Japan, where the recent bird protection treaty is resulting in more research into conservation.

Concern was expressed about the increasing number of plastic pellets being ingested by seabirds. Dr. WARHAM reported that it is even evident in New Zealand, where many are picked up by White-faced Storm-petrels *Pelagodroma marina*. The prions *Pachyptila* sp. also pick up pumice from volcanic eruptions, and young albatrosses *Diomedea* sp. may be fed a variety of materials. It was reported that pelicans are proving particularly vulnerable to plastic fishing line and the plastic rings used to link the tops of beer cans, in which they become entangled.

It emerged during the discussion that there were really too few European ornithologists present for a useful discussion of continental surveys, but that there was little general enthusiasm for either further breeding surveys at the present time, or a census of wintering gulls proposed by Dr. P. ISENMANN. The latter presents considerably more

difficulties in the north of Europe, where the number of birds is much larger and they are much more widely distributed than in the south, and it was felt that considerably more preparatory work with local surveys and the development of census techniques is required before they are adopted more widely.

W. R. P. Bourne, Secretary.

Members of the Committee

Prof. Dr. K. H. Voous (Chairman), Maasdamlaan 28, 1272 EM Huizen, Netherlands.
Dr. W. R. P. Bourne (Secretary) Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB9 2TN, Scotland, U.K.
Dr. R. G. B. Brown, Canadian Wildlife Service, Bedford Institute, P.O.Box 1006, Darmouth, Nova Scotia, B2Y 4A2 Canada.
Dr. J. P. Croxall, S.C.A.R., British Antarctic Survey, Madingley Road, Cambridge, CB3 OET, England, U.K.
Dr. P. Devillers, Institut Royal des Sciences Naturelles de Belgique, 13 rue Vautier, 1040 Bruxelles, Belgium.
Dr. F. Goethe, Kirchreihe 19 B, 2940 Wilhelmshaven, West-Germany.
Dr. J. H. Jehl, Hubbs-Sea World Research Institute, 1700 South Shores Road, Mission Bay, San Diego, California, 92109 U.S.A.
Dr. G. Johnstone, Antarctic Division, 568 St. Kilda Road, Melbourne, Victoria, 3004 Australia.
Mr. C. Jouanin, Muséum National d'Histoire Naturelle, 55 rue de Buffon, 75 Paris V, France.
Dr. J. L. Mougin, Museum National d'Histoire Naturelle, 55 rue de Buffon, 75 Paris V, France.
Mr. C. J. R. Robertson, New Zealand Wildlife Service, Department of Internal Affairs, Private Bag, Wellington, New Zealand.
Prof. Dr. W. R. Siegfried, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, C.P., 7700 South Africa.
Dr. K. Vermeer, Canadian Wildlife Service, Westham Island, P.O.Box 340, Delta, British Columbia, V4K 3Y3 Canada.
Dr. G. E. Watson, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560 U.S.A.

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The Regulation of the Annual Cycle of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*

Donald S. Farner

Introduction

The White-crowned Sparrow is one of the five species of the widespread New World fringillid genus *Zonotrichia*. Among the five races of *Zonotrichia leucophrys*, *gambelii* is a typical middistance migrant. Its principal breeding range is in western Canada and Alaska. Its principal wintering range extends widely through southwestern United States and northern Mexico with isolated wintering populations occurring as far north as the state of Washington. (Banks, 1964; Cortopassi & Mewaldt, 1965; Lewis et al., 1968; Mewaldt & Farner, 1953). Because of its abundance and adaptability to captivity this race has been the subject of extensive investigations in both field and laboratory (for selected reviews, see Blanchard & Erickson, 1949; Farner, 1964, 1966, 1970, 1975; Farner & Follett 1966, 1978; Farner & Lewis, 1971, 1973; King & Farner, 1966; Mewaldt et al., 1968; Oksche & Farner, 1974).

The White-crowned Sparrow, like other species that inhabit periodic environments of mid and high latitudes, has evolved a control system that generates an annual cycle in which the reproductive effort occurs at a time when environmental conditions are optimal for survival of young and adults. Since the reproductive effort is certainly a most important feature of the annual cycle, it follows that the components and functions of the control system that fix the time of reproduction are continuous targets of natural selection. However, the fitness of the individual White-crowned Sparrow depends also, to varying degrees, on the precision of the timing of other events and functions in the annual cycle. To consider a single event or phase out of the context of the entire cycle can result in misleading conclusions.

It is both useful and meaningful to examine the annual cycle from the aspect of the temporal separation of ergonically expensive functions, such as reproduction, molt and migration; available trophic resources; and day-light hours available for their exploitation. A precise synthesis of these aspects with respect to the nature and adaptiveness of the control system has not been achieved for any species. This presentation is, in a sense, an assessment of progress toward this goal with the White-crowned Sparrow. The assessment is directed primarily towards the race *gambelii* although we have used cautiously other races of *Z. leucophrys* and other species as well.

The reference above to *Z. l. gambelii* as a "typical" middistance migrant is almost certainly semantically misleading. Species have doubtless invaded mid and high latitudes many times independently. Relationships among the neural and endocrine components of the control systems were altered by selection with an enhancement of fitness with respect to the new environments. Thus it seems highly probable that the control systems for similar annual cycles may differ substantially from a physiologic aspect (Farner, 1964, 1970, 1975; Farner et al. 1977; Sansum & King, 1976).

Department of Zoology, University of Washington, Seattle, Washington, U.S.A.

The annual cycle

As noted above, it is informative to examine the annual cycle from the aspect of rates of expenditure of energy. For this purpose the following somewhat arbitrary phases can be delineated (Fig. 1): (1) Winter. relatively high mean daily caloric expenditure for thermoregulation, here estimated for a no-longer existing wintering population in the Snake River Canyon in eastern Washington (MAHONEY, 1976). (2) Prenuptial molt. (3) Vernal migration. Hyperphagia, and pre- and intramigratory fat deposition that provide energy for nocturnal migratory flight. (4) Breeding. The rate of energy expenditure in Figure 1 is from the estimates of MALONEY (1976) for an Alaskan breeding population. (5) Postnuptial molt. (6) Autumnal migration. Similar to (3) but somewhat less intense.

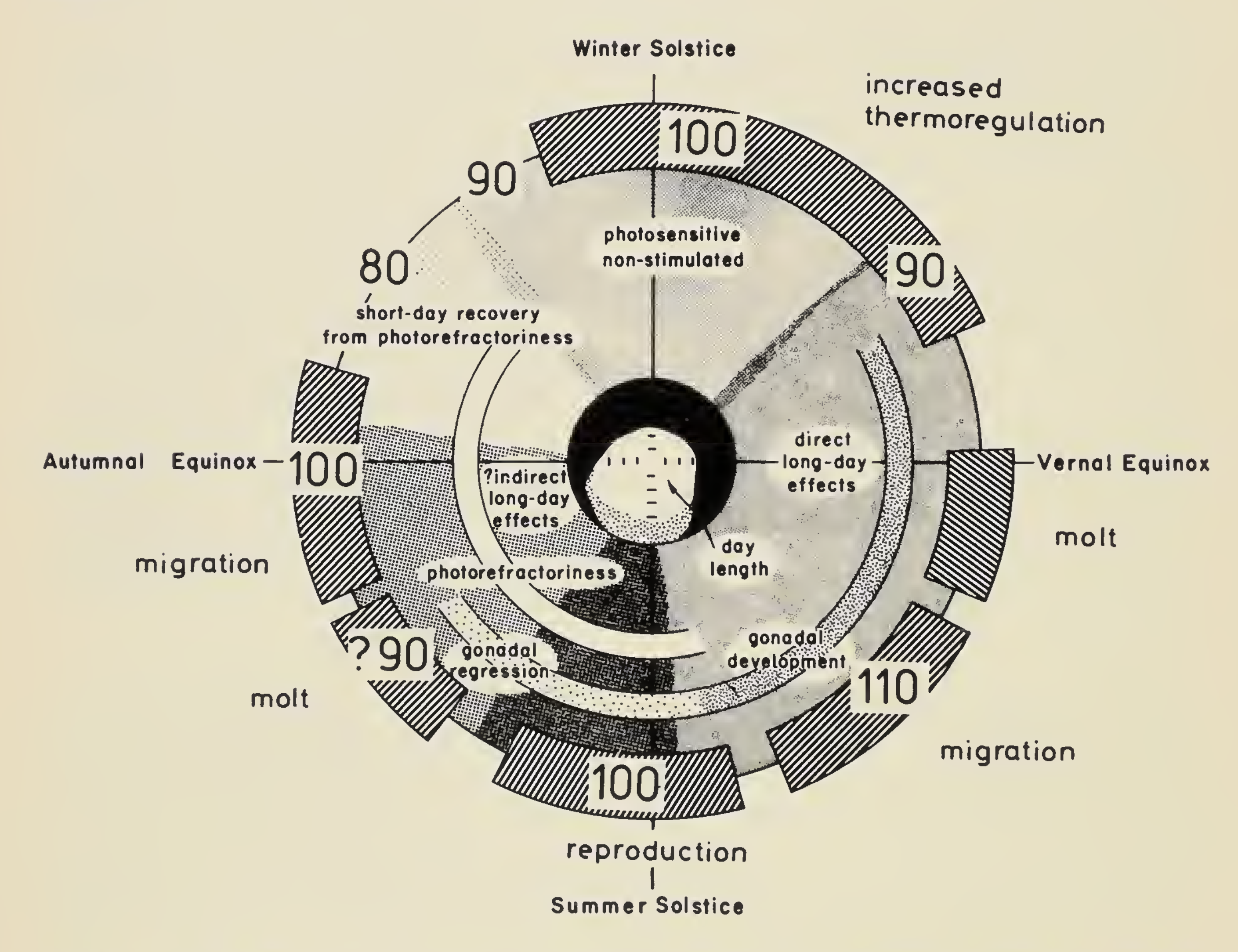


FIGURE 1. The annual cycle of *Zonotrichia leucophrys gambelii*. The peripheral numbers are estimates of mean daily expenditures of energy in kJ per day for the indicated phases of the cycle. See text for sources of information and bases for estimates. Modified from FARNER (1964) by Miss D. VAIHINGER.

It must be emphasized that all estimates in Figure 1 are relatively crude approximations.

The estimates for the mean daily energy costs for migration require explanation. Since we have no directly pertinent data for *Zonotrichia* the estimates rest on several assumptions and calculations. Although some populations may have longer routes, the estimates in Figure 1 are based on a total migratory flight of 3500 km spread over a period of 60 days for vernal migration and 70 days for fall migration. The estimated cost of flight has been

added to the estimated non-flight energy expenditure for the period and the sum divided by 60 and 70 for the vernal and autumnal periods, respectively. With additional assumptions the costs of migratory flight have been estimated (1) from the measurements of Tucker (1968) on flight by *Melopsittacus undulatus* in a wind tunnel; (2) on indirect measurement of energy cost of flight by *Fringilla coelebs* and *Pyrrhula pyrrhula* (Dolnik, 1970, 1975a; Dolnik & Gavrilov, 1971a; Dolnik et al., 1963); the equation of Tucker (1971) for the cost of flight at optimal air speed and his equation (1973) for energy required at minimum cost of transport; (4) from the equation of Pennycuick (1969) that relates energy cost of flight to body weight and lift-drag ratio; (5) the equation of Kendeigh et al. (1977) for energy cost of flight; (6) the equation of Berger & Hart (1974) for maximum power in flight; and (7) from calculations for *Zonotrichia albicollis* by Helms (1968) based on data on weight loss by Nisbet et al. (1963). For the vernal migratory period these calculations yield estimates ranging from 95 to 140 kJ per day. The daily expenditure varies, of course, with respect to migratory activity. The total expenditure for a day that includes a migratory flight of 200 km may exceed 135 kJ somewhat as compared with 80 kJ for a day with no migratory flight. In terms of energy intake the bird spreads the cost of migratory flight by the use of previously stored fat. In vernal migration the White-crowned Sparrow begins a migratory flight with a reserve of 5–6 grams of fat; in autumnal migration this reserve is about three grams (King, 1961a, 1963, 1967; King et al., 1963). A gram of fat yields energy sufficient for a flight of about 140 kilometers for a bird of the size of the White-crowned Sparrow (Pennycuick, 1969).

The estimate of the rate of energy expenditure during postnuptial molt is expecially tenuous because of a lack of sufficient information directly pertinent to the White-crowned Sparrow. The estimate is based on the energy cost of molting in *Passer domesticus* (Blackmore, 1969; Kendeigh et al., 1977), *Fringilla coelebs* (Gavrilov & Dolnik, 1974; Kendeigh et al., 1977) and *Zonotrichia albicollis* (Helms, 1968). Although the cost of the growth of new feathers can be estimated reasonably well, the estimation of the daily rates of expenditure through the molting period is confounded by changing thermoregulatory requirements, reduced motor activity (e.g. Dolnik, 1976b) and possibly by an increased food intake to provide cystein and cystine for new feathers (Blackmore, 1969; Gavrilov & Dolnik, 1974; Kendeigh et al., 1977). The estimate for the molting period in Figure 1 is doubtless the least certain of the estimates.

A few comments concerning the rate of energy expenditure during the reproductive period are desirable. The estimates of Mahoney (1976) do not specifically include the costs of development of the gonads and the production of eggs. The energetic costs of testicular development, which actually occur before and during migration, are trivial when prorated over the entire period of development (King, 1973). Most of the development of the ovary and oviduct occurs after the female arrives in the breeding territory but probably does not exceed 3 kJ per day (King, 1973). The cost of a five-egg clutch is 70–80 kJ (King, 1973; personal communication). Because the phase of rapid deposition of yolk is of the order of 5–6 days the maximum energy per day used for the synthesis of yolk is about 18.6 kJ (King, personal communication), some fraction of which is probably drawn from fat reserves (Wingfield & Farner, 1978 a,b). A recent sophisticated investigation of the cost of incubation by female *Z. l. oriantha* (Walsberg & King, 1978) shows convincingly, and quite contrary to frequently expressed beliefs, that the metabolic rate of the incubating

female is actually somewhat lower than that of a perching bird under the same ambient conditions. Caution must be exercised, however, in extending this conclusion to other species. By direct measurement of oxygen uptake and carbon-dioxide release BIEBACH (1977) has shown that the rate of energy expenditure by an incubating female *Sturnus vulgaris* is about 20% greater than that of a non-incubating female at the same temperature.

Indeed, in the White-crowned Sparrow, the lower level of fat reserves and the intensity of motor activity during the feeding of the young suggest that this is the time of the greatest expenditure of energy during the reproductive period. DOLNIK (KENDEIGH et al., 1977) has estimated that Chaffinches expend slightly more than 8 kJ per day in the feeding of young. For the White-crowned Sparrow one can, nevertheless, cautiously conclude that deviations from the estimated daily expenditure of 100 kJ per day are probably not very great. Because of the abundance of trophic resources and the very long days in which they can be exploited, it can be surmized that accomodation to surges in daily energy requirement is relatively easy.

An important feature of the annual cycle is the role of fat reserves in ergonically intense functions in which the rate of energy expenditure may temporarily exceed the rate of energy intake, or in which intake of energy is not possible. The conspicuous examples, of course, are the vernal and autumnal periods of migratory fat deposition (KING, 1961a, 1963, 1972; KING & FARNER, 1976). White-crowned Sparrows also deposit fat in winter as a reserve against temporary increases in thermoregulatory requirements, especially in long winter nights (KING & FARNER, 1966). Although the deposition of fat is affected by a number of factors, it is clear that extensive deposition invariably involves an active, programmed hyperphagia in which an appestat is set to maintain or restore a higher level of fat reserves (KING, 1961b, 1972). Although the adaptiveness of the annual cycle in fat reserves is clear, the physiology of its control and regulation remains relatively unsatisfactory (KING, 1972).

Despite the crude nature of the estimates of daily rates of energy expenditure in Figure 1, two significant facets become clearly apparent: (1) There is rigid temporal separation of ergonically expensive functions, a principle that holds extensively, but not completely, for small birds. (2) The differences in mean rates of daily energy expenditure among the phases of the annual cycle, perhaps somewhat exaggerated in Figure 1, are relatively small. This is accomplished by a control system that separates ergonically expensive functions and that regulates the geographic position of the bird through the course of the cycle towards a minimization of costs of thermoregulation. This principle also appears to hold for non-migratory species as is illustrated well for *Passer domesticus* by KENDEIGH et al. (1977).

Information used in the control of the annual cycle

Because the initiation of gonadal development occurs while White-crowned Sparrows are still in the wintering areas and because the onset and course of migration must be controlled for a temporally appropriate arrival in the breeding area, the control system must use information of a reliable predictive nature (FARNER, 1964, 1970, 1975). The basic information used by the control system is day length. Long days, either natural or artificial, induce directly gonadal development, complete in the male but only partial in the

female; prenuptial molt; vernal migratory fattening and migratory behavior. None of these functions occur in birds held on short days for more than two years. Long days induce indirectly the development of photorefractoriness, and hence the termination of gonadal function; of post-nuptial molt; and of autumnal migratory fattening and migratory behavior. These events also fail to occur in White-crowned Sparrows held on short days. In *Fringilla coelebs* there is a very precise temporal relationship between the rate of testicular development, which is a function of day length, and the onset of photorefractoriness, postnutial molt, and autumnal migration (Dolnik, 1975a, b; 1976a; Dolnik & Gavrilov, 1972; Gavrilov & Dolnik, 1974). Our less extensive information on the White-crowned Sparrow (D. S. Farner, R. S. Donham and R. A. Lewis, unpublished) indicates similarly precise relationships. The relationship between regression of the gonads and the post-nuptial molt, however, requires additional comment. Field observations (Morton et al., 1969; Wingfield & Farner, 1977, 1978a, b) and the results of some laboratory experiments (Farner, 1964; D. S. Farner, R. S. Donham, unpublished results) suggest a close functional relationship between regression of the gonads and the onset of molt. However, White-crowned Sparrows held on 12L 12D failed to molt following regression of the testes, and photorefractory birds held for six years on 20-hour days molted somewhat irregularly in the absence of testicular cycles.

The adaptiveness of the photorefractory state in the discontinuation of gonadal function and consequently in the avoidance of unseasonal reproductive effort is clear. However, its physiologic basis remains unknown (Farner, 1964, 1975; Farner & Follett, 1966, 1968). Photorefractory males held as long as six years on long days fail to undergo testicular development (D. S. Farner, R. S. Donham, R. A. Lewis, unpublished; see also Sansum & King, 1976). The short days of late autumn thus constitute essential information in the control of the annual cycle.

The phenological schedule of the breeding area varies somewhat from year to year and White-crowned Sparrows adjust the onset of reproductive activity accordingly. This means that, in addition to day length, the control system must use additional sources of information to effect a fine adjustment of the onset of reproductive activity.

Examined in detail, the control of the annual cycle involves an interplay of external and internal information that is translated into neural and hormonal information (Farner, 1970, 1978; Farner & Lewis 1971):

External information

Primary external information:

As emphasized above day length is the essential and most important external source of information. Theoretically, there are at least three ways in which the annual photocycle can be used as a source of information: (1) As a Zeitgeber for an endogenous circannual cycle (See Internal information below). (2) As a direct driver, via the hypothalamus, of the functions that cause gonadal growth, hyperphagia, migratory behavior, etc. (3) As activator of the first in a chain of events that follow each other automatically through the completion of autumnal migration. 2. and 3. are not necessarily mutually exclusive. And, indeed, a combination of 2. and 3. seems to provide the best rationalization for our present knowledge of system.

Secondary external information:

These sources of information are designated as secondary since they are effective in the control of the annual cycle only after the cycle has been induced by long days.

(1) Modifying information alters the temporal course of the cycle, especially during the latter part of vernal migration and after arrival in the breeding area, but also in autumnal migration. Included in this category are environmental temperature, trophic conditions, the physical structure of the environment, for example, the depth of snow on the breeding territories (MORTON, 1976; OAKESON, 1954; D. S. FARNER, unpublished observations). Other modifying information associated with the breeding territory, perhaps interaction with the female, extends the time during which the testes are fully functional and increases the rate of secretion of gonadotropins and testosterone.

(2) Essential supplemental information is of special importance with respect to the female since long days alone can induce development of the ovary only to the beginning of the yolk-deposition phase (FARNER et al. 1966; FARNER & LEWIS, 1971; KING et al. 1966; KERN, 1972). This final phase in the development of the ovary, which occurs in upwards of 10 days, requires essential supplemental information derived apparently from the breeding territory and interaction with the territory-holding male. However, the situation is apparently complex since long-day treatment of eyeless females leads to an apparently normal deposition of yolk and development of the oviduct (YOKOYAMA & FARNER, 1976). Thus it may be that inhibitory external information normally counteracts partially the effect of long days so that the final stage of development of the ovary is not attained until the inhibitory information is no longer received.

Internal information

Although the distinction is not alway clear, it is useful to recognize two general categories of intrinsic information, both of which are often modified or synchronized by external information.

Endogenous, self-sustaining rhythms:

It is increasingly clear that the temporal organization of life involves numerous or many self-sustained endogenous oscillating functions. In birds extensive attention has been given to circadian and circannual rhythms. But others may also prove to be of importance.

(1) Circadian rhythms. These rhythms, which have natural periods of approximately 24 hours, are entrained into precise daily cycles by the daily environmental photocycle (Zeitgeber). They are of fundamental importance in the basic temporal organization of organisms. (For a review of circadian functions in birds, see GWINNER, 1975). In the White-crowned Sparrow, it is clear for example, that the mechanism that measures day length contains a circadian component (FARNER, 1975; SANSUM & KING 1975; TUREK, 1972).

(2) Circannual rhythms. There is an abundance of evidence from a number of passerine species concerning the existence of such rhythms in birds held on constant day lengths, often 12 hours (e.g., BERTHOLD, 1974, 1977; GWINNER, 1975, 1977a, b). This is supportive of a hypothesis that annual cycles, including that of reproduction, of photoperiodic species of birds are endogenous circannual cycles for which the role of the environmental

photocycle is that of a Zeitgeber (Aschoff, 1955; Dolnik 1974, 1976a; Gwinner 1977 a, b; Immelmann, 1967). Although the physiologic basis of the circannual rhythms thus far described is entirely unknown, the hypothesis is nevertheless attractive. However, at least in its simplest form it appears to be inconsistent with several of the physiologic properties of the control system of the White-crowned Sparrow (Farner & Lewis, 1973; Farner & Follett, 1978; King & Farner, 1974; Sansum & King, 1976).

The information used by the female requires additional comment since the time span of the fully functional ovary is considerably briefer but more adjustable than that of the testes (Kern, 1972; King et al., 1966; Wingfield & Farner, 1978b). It is therefore the female that ultimately provides the fine adjustment of the time of onset of the reproductive effort. This is, of course, adaptive in the sense of the relatively greater cost of the clutch in comparison with cost of production spermatozoa (King, 1973). The role of day length in the development of the functional ovary is dual: long days are essential for development up to the onset of the phase of yolk deposition. By induction of the functional testis and consequent sexual behavior of the male they provide indirectly one of the sources of essential supplemental information for the femal.

Still undefined with respect to sources of information, is the phenomenon of renesting when a clutch or nest is lost early in the breeding season. In males there is a recrudescense of the testes, doubtless due to an increase in secretion of FSH, and increases in the plasma levels of LH and testosterone. In females the ovary quickly returns to full functional state, doubtless because of increased secretion of gonadotropins (Wingfield & Farner, 1978b, 1979).

The control of the annual reproductive cycle

When male White-crowned Sparrows that have been held under short days, either under natural winter conditions or artificially in the laboratory, are exposed artificially to long days of constant duration, the testes grow as a logarithmic function of time until they approach half of maximum size after which the growth rate becomes progressively lower (Farner & Wilson, 1957). Since LH is apparently solely steroidogenic (Brown et al., 1975), at least the logarithmic phase of development may be assumed to be caused by FSH. A similar pattern of ovarian growth occurs in artificially photostimulated females but, as noted above, it ceases before the onset of deposition of yolk (Farner et al., 1966). The logarithmic growth rate is a positive function of the duration of the long days to which the bird is exposed (Farner & Wilson, 1957). This indicates that the control system must somehow measure day length.

In the White-crowned Sparrow, as in at least some other photoperiodic species (Farner, 1975; Farner & Lewis, 1971; Farner & Follett, 1978), the mechanism contains a circadian oscillator. Results from a number of experiments (Follett et al., 1974; Farner, 1975) are consistent with a so-called internal coincidence model, first proposed by Bünning (1936) and subsequently refined by Pittendrigh & Minis (1964). This model, as applied to the White-crowned Sparrow, assumes the involvement of an entrained circadian oscillation in photosensitivity, normally entrained so that its photosensitive phase occurs approximately between hours 8 and 22 after dawn. When the day is sufficiently long to extend into the photosensitive phase the photoperiodic responses, e.g. increased secretion of gonadotropins, gonadal growth, migratory hyperphagia and fatten-

ing, and migratory behavior are induced. It is firmly emphasized, however, that this is only a model and that there is no direct evidence for an oscillation in photosensitivity.

Other models may be applicable. DOLNIK (1976a), for example has proposed an internal coincidence model for *Passer domesticus* and for *Fringilla coelebs*. However, at least in its present form, it makes predictions that are inconsistent with results that we have obtained with experiments on the White-throated Sparrow and with the House Sparrow. MEIER and his colleagues (e.g. MEIER, 1976) have developed a sophisticated internal coincidence model for the photoperiodic control system of the White-crowned Sparrow. The model is complex in that it involves separate photoinducible phases, one for LH and another for FSH and prolactin, and rests further on phase relationships between daily cycle in plasma concentrations of corticosterone and prolactin. Because we still lack microassays for plasma levels of FSH and prolactin in *Zonotrichia* we have been unable to test the model in the White-crowned Sparrow. Nevertheless, it seems highly probable that prolactin is somehow involved in the induction and control of migratory fattening and migratory behavior (MEIER et al., 1965).

The photoreceptors of the photoperiodic control system of the White-crowned Sparrow are encephalic. Such encephalic receptors, first described functionally by BENOIT (1935a, b) more than four decades ago, may well be general among birds. In the White-crowned Sparrow they are probably morphologically unspecialized neurones that lie extensively, although probably not exclusively, in the ventral hypothalamus (YOKOYAMA et al., 1978). Since light from the tip of a single fine light-conducting fiber can induce testicular growth (YOKOYAMA et al., 1978) and migratory behavior (YOKOYAMA & FARNER, 1978) comparable to that of an intact bird held on long days, it must be assumed that the system has a very substantial capability for amplification. Results of investigations by MENAKER and his associates (MCMILLAN et al., 1975) make it extremely unlikely that retinal receptors have any stimulatory role whatsoever in the photoperiodic control system. On the contrary, as noted above, information from the retina may have an inhibitory function (YOKOYAMA & FARNER, 1976).

It appears that elements of two nuclear regions of the hypothalamus are essential for the control of gonadotropic function in photoperiodic species of birds, including the White-crowned Sparrow: (1) Tuberal region, including the infundibular-nucleus complex with which, in addition to others, the photoreceptor system is probably associated (OKSCHE & FARNER, 1974; STETSON, 1969; WILSON, 1967; YOKOYAMA, 1976). (2) The preoptic region (ASSENMACHER, 1958; FOLLETT, 1973; NOVIKOV & RUDNEVA, 1964; OKSCHE, 1978; OKSCHE & FARNER, 1974). Under photoperiodic stimulation neuronal elements of these two regions interact in a manner that is not yet understood. The result of this interaction, however, is the transfer of gonadotropin-releasing neurohormones from the endings of axions of the tuberohyphophysial tract in the median eminence into blood capillaries of the portal system of the anterior pituitary gland. These neurohormones then induce the synthesis and release of the gonadotropic hormones. The elevated plasma levels of gonadotropic hormones in the photostimulated bird are limited by negative feedback effects of sex hormones and adjusted by the effects of modifying and essential supplemental information in the hypothalamus, both mediated through the hypophysis (Fig. 2).

It is clear that our knowledge of the above described conversion of day length as external information, first into neural information, and finally into altered plasma levels of pituitary

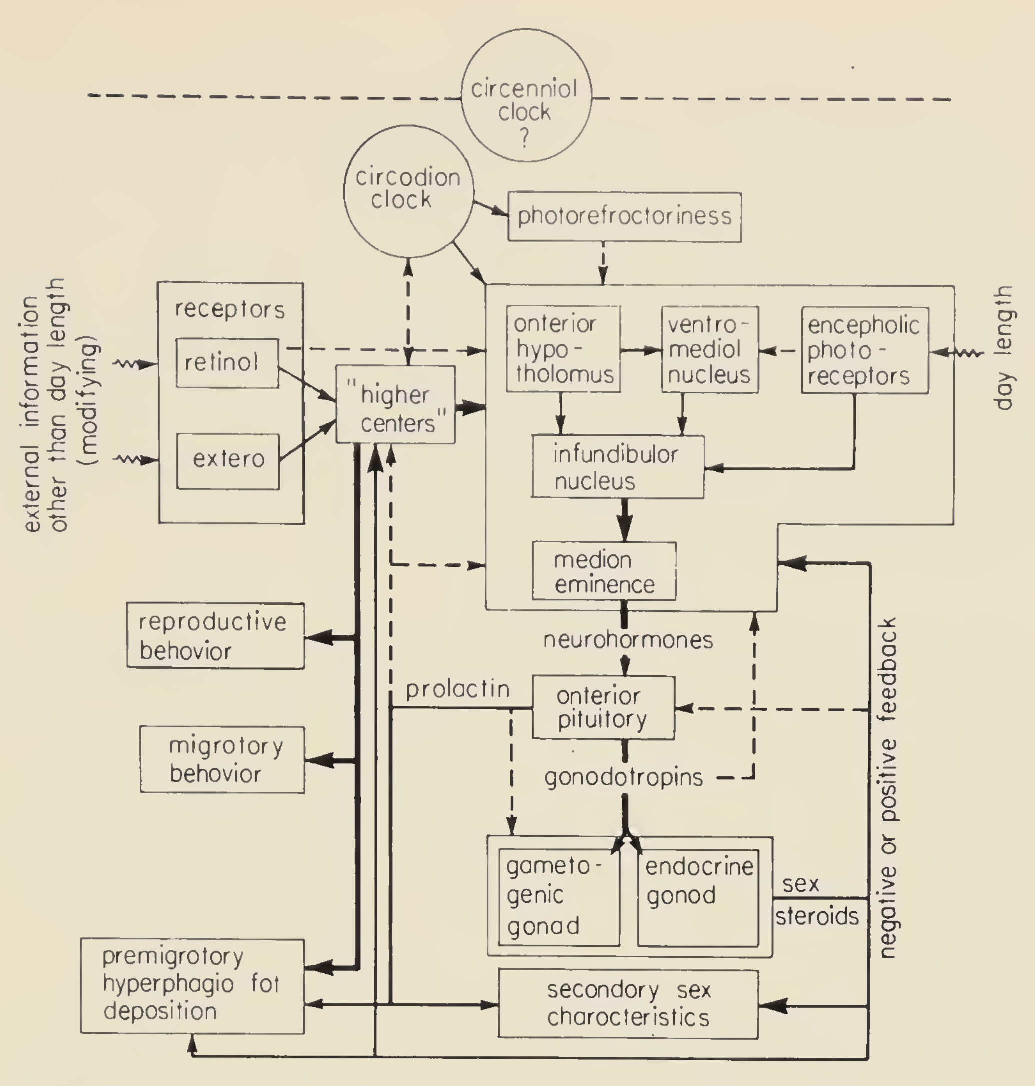


Figure 2. Selected components and functions of the system that controls the annual reproductive cycle and related functions in *Zonotrichia leucophrys gambelii*. Prepared by Dr. J. C. Wingfield.

hormones is sketchy. The results of investigations accumulated thus far serve largely to define and identify the fascinating and challenging research problems that lie before us.

The endocrine effects of modifying and essential supplementary information

Because of the ease with which day length can be manipulated experimentally, its role in the endocrine control of reproductive function has been extensively quantified (Farner, 1975; Farner & Follett, 1978). The endocrine effects of modifying and essential supplementary information, especially in a feral species such as the White-crowned Sparrow, are much more difficult to assess. However, comparison of plasma levels of hormones and hormonally induced functions in photoperiodically stimulated captive birds with those of birds in breeding territories permit crude but useful comparisons (Wingfield & Farner, 1977, 1978a, b, 1979; Farner, 1978).

The most striking effect of essential supplementary information is in the female. As already noted, the ovary fails to reach the final stage of development under photoperiodic stimulation alone. Although we have thus far been unable to measure FSH in plasma and therefore lack direct evidence, it is reasonable to assume that this is due primarily to a deficit of FSH although the plasma level of LH attained by photostimulated captive females is somewhat lower than that of breeding females under natural conditions.

Captive male White-crowned Sparrows, unlike females, develop fully functional gonads when held on long days. Nevertheless, comparisons with breeding males demonstrate effects of modifying information. The testes of the latter develop to somewhat greater size and remain fully developed for a longer time. This doubtless reflects a somewhat higher of secretion of FSH over a longer span of time. The level of LH is higher and the resulting level of testosterone is conspicuously greater. Since the latter has a role in maintenance of spermatogenesis (e.g., DESJARDINS & TUREK, 1977), it may account for the longer persistence of the functional testis (WINGFIELD & FARNER, 1979). The mechanisms by which non-photoperiodic environmental information alters the basically photoperiodic pattern of endocrine control of reproduction remain one of the most challenging research areas in avian endocrinology and ethology.

Resume

The control system for the annual cycle of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii,* is adaptive in that young are produced at a time when conditions are optimal for survival of the young and their parents. Ergonically expensive functions are separated in time and are so arranged that the daily expenditure of energy does not vary widely during the course of the cycle. Use of controlled reserves of fat permit temporary high rates of expenditures with relatively smaller increases in energy intake distributed over a greater span of time.

The principal and basic source of information used by the control system, and particularily by the hypothalamus, is day length which the system measures by a mechanism with a circadian component. Photoreception is encephalic. The receptors occur largely, if not exclusively, in the hypothalamus. Long days induce directly, by increases in plasma levels of gonadotropins, the development of the gonads and also in a more complex manner, vernal migration, including pre- and intramigratory hyperphagia and fat deposition. The fine temporal adjustment of the onset of the breeding season involves modifying environmental information. The photostimulated female requires additional essential supplementary information for completion of the development of the reproductive system and accompanying sexual behavior.

Reproductive function is discontinued by the development of a photorefractory state in which the secretion of gonadotropin is drastically curtailed. It is apparently an indirect effect of the long days of spring and early summer. Photorefractoriness is eliminated by some effect of shorter days in autumn. Other apparently indirect effects of long days are the postnuptial molt and autumnal migration.

The available information on the control of the annual cycle is not consistent with the hypothesis that the role of day length is that of a Zeitgeber for an endogenous circannual cycle although it may prove to be consistent with a rather fundamental modification thereof.

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In memoriam Oskar Heinroth

KONRAD LORENZ

OSKAR HEINROTH ist der Vater der vergleichenden Verhaltensforschung oder Ethologie. Diese Forschungsweise zu definieren ist nicht schwer. Sie kennzeichnet sich dadurch, daß sie auf das Verhalten von Tieren und Menschen dieselben Fragestellungen und Methoden anwendet, die in allen anderen Zweigen der Biologie seit Charles Darwin selbstverständlich waren. Es ist keine falsche Bescheidenheit von meiner Seite, wenn ich den Ehrentitel Vater der Ethologie ablehne, er gebührt wirklich OSKAR HEINROTH; alle wesentlichen Erkenntnisse, auf denen sich die heutige vergleichende Verhaltensforschung aufbaut, finden sich bei ihm meistens expressis verbis, seltener auch zwischen den Zeilen, aber auch dort deutlich genug. HEINROTH hat auch die Anwendbarkeit vergleichender Verhaltensforschung auf menschliche Belange voll erkannt, ja sogar deren wichtigste Ergebnisse vorausgeahnt. Er sagt am Schluß seiner klassischen Arbeit „Beiträge zur Biologie, insbesondere Psychologie und Ethologie der Anatiden“: „Die Sauropsidenreihe hat hier ganz ähnliche Affekte, Gebräuche und Motive entwickelt, wie wir sie bei uns Menschen gewöhnlich für verdienstvoll, moralisch und dem Verstand entsprungen heißen. Das Studium der Ethologie der höheren Tiere – leider ein noch sehr unbeackertes Feld – wird uns immer mehr zu der Erkenntnis bringen, daß es sich bei unserem Benehmen gegen Familie und Freunde, beim Liebeswerben und ähnlichem um rein angeborene, viel primitivere Vorgänge handelt, als wir gemeinhin glauben.“

Um die Bedeutung HEINROTHS und auch die seines amerikanischen Bruders im Geiste, CHARLES OTIS WHITMAN, richtig einzuschätzen, muß man die Lehrmeinungen bedenken, die in der Psychologie und Soziologie zu jener Zeit herrschten. Es war der Meinungsstreit zwischen zwei großen Psychologen-Schulen, der das Eindringen biologischen Denkens in die Psychologie verhinderte, ja zu Teil noch verhindert. Die Erbitterung, mit der dieser Meinungsstreit ausgefochten wurde, war vor allem durch die weltanschauliche Verschiedenheit der Gegner genährt. Die Schule der Zweckpsychologie (purposive psychology), die vor allem von WILLIAM MAC DOUGALL und späterhin von EDWARD CHASE TOLMAN vertreten wurde, postulierte einen außernatürlichen Faktor: Der „Instinkt“ wurde als ein Agens betrachtet, das einer natürlichen Erklärung weder bedürftig, noch zugänglich ist. „Wir betrachten den Instinkt, aber wir erklären ihn nicht“, schrieb BIERENS DE HAAN noch 1940. Diesem Begriff des Instinktes haftete stets auch die Vorstellung von seiner Unfehlbarbeit an. MACDOUGALL lehnte alle mechanistischen Erklärungen des Verhaltens ab, z. B. betrachtete er es als eine Auswirkung des Instinktes, wenn Insekten zweckmäßigerweise dem Hellen zustreben, die Möglichkeit einer mechanistischen Erklärung durch Tropismen gab er nur dort zu, wo diese Tiere höchst unzweckmäßigerweise in ein brennendes Licht fliegen. In allem, was sie tun, verfolgen die Tiere, nach Meinung MACDOUGALLS und seiner Schule einen Zweck (purpose), und dieser Zweck ist von ihrem außernatürlichen und untrüglichen Instinkt gesetzt.

Die Schule des Behaviorismus (von engl. behaviour = Verhalten) kritisierte mit Recht die Annahme außernatürlicher Faktoren als unwissenschaftlich und stellte die Forderung

A-3422 Altenberg, Lorenzgasse 2, Österreich.

nach ursächlicher Erklärung. In ihrer Methodik suchte sie sich möglichst weit von derjenigen der Zweckpsychologen abzusetzen. Sie betrachtete das kontrollierte Experiment als einzig legitime Wisssensquelle. Empirische Methoden sollten an Stelle philosophischer Spekulation treten.

Mit Ausnahme einer gewissen Geringschätzung der einfachen Beobachtung enthielt dieses Programm keinen methodologischen Fehler, dennoch zeitigte es eine böse Folge: Es konzentrierte das gesamte Forschungsinteresse auf jene Anteile tierischen und menschlichen Verhaltens, mit denen sich am besten experimentieren ließ – und führte so zum Erklärungs–Monismus.

Aus einer Kombination der Assoziationslehre WILHELM WUNDTS mit der zur Zeit in der Psychologie herrschenden Reflex-Theorie, sowie mit den Ergebnissen I. P. PAWLOWS ließ sich leicht ein Verhaltensmechanismus abstrahieren, dessen Beschaffenheit ihn zum idealen Objekt experimenteller Forschung stempelte, nämlich die sogenannte bedingte Reaktion.

Zu seiner Zeit war das Verfahren der Behavioristen mit seiner korrigierenden Kritik an den Meinungen der Purposivisten durchaus begrüßenswert. Unmerklich aber schlich sich ein verderblicher logischer Fehler in das behavioristische Denken ein: Weil man nur die Lernvorgänge experimentell untersuchen kann und alles Verhalten experimentell untersucht werden muß, dann muß, so schloß die behavioristische Lehrmeinung, alles Verhalten erlernt sein – was natürlich nicht nur logisch falsch, sondern auch faktisch ein vollkommener Unsinn ist.

Das Wissen um die gegnerische Meinung und die berechtigte Kritik an ihr drängten sowohl Purposivisten wie Behavioristen in extreme Stellungen, die weder die einen noch die anderen sonst eingenommen hätten. Waren die einen von einer mystischen Ehrfurcht vor dem ,,Instinkt" erfüllt und trauten dem Angeborenen übergroße Leistungen, ja sogar Unfehlbarkeit zu, so leugneten die anderen seine Existenz. Die Purposivisten, die offene Augen für angeborene Verhaltensweisen hatten, hielten alles Instinktive für unerklärlich und weigerten sich, wie BIERENS DE HAAN, seine Kausalanalyse auch nur zu versuchen. Diejenigen, die sehr wohl fähig und bereit gewesen wären, eine solche analytische Forschung in Angriff zu nehmen, leugneten die Existenz von irgend etwas Angeborenem und erklärten dogmatisch alles Verhalten für erlernt. Das wahrhaft Tragische an dieser historischen Situation liegt darin, daß die Purposivisten, vor allem MACDOUGALL selbst, Tierkenner waren und ein gutes Allgemeinwissen über tierisches Verhalten besaßen, das den Behavioristen auch heute noch abgeht, da sie die einfache Beobachtung für unnötig, ja für ,,unwissenschaftlich" halten. Es kommt einem wahrlich der Ausspruch Fausts in den Sinn ,,Was man nicht weiß, das eben brauchte man, und was man weiß, kann man nicht brauchen".

Die Stärke der hemmenden Wirkung, die der eben besprochene Meinungsstreit ausübte, ist am besten dadurch bewiesen, daß es nicht Psychologen, sondern zwei Zoologen waren, die den gordischen Knoten durchtrennten: OSKAR HEINROTH und CHARLES OTIS WHITMAN. Beide waren Liebhaber einer bestimmten Tiergruppe, WHITMAN der Tauben, HEINROTH der Entenvögel (Anatidae). CHARLES OTIS WHITMAN hat schon 1889 den Satz ausgesprochen, ,,Instinkte und Organe müssen vom gemeinsamen Gesichtspunkt der phyletischen Abstammung erforscht werden" (Instincts and organs are to be studied from the common viewpoint of phyletic descent). OSKAR HEINROTH hat dieselbe Erkenntnis zwar etwas später, aber völlig unabhängig von WHITMAN gewonnen, auch hat er, wie ich

glaube, die Folgerungen aus dieser Erkenntnis in einem weiteren Kreise gezogen, als WHITMAN es je tat. Das kommt wahrscheinlich daher, daß HEINROTH mehr Tiere und Tiergruppen genau kannte als WHITMAN, und als berufsmäßiger Tiergärtner auch über ihr Verhalten Genaueres wußte. So machte er die im wahrsten Sinne des Wortes epochemachende Entdeckung, daß es Bewegungsweisen gibt, deren Ähnlichkeit und Verschiedenheit von Art zu Art, von Gattung zu Gattung, ja von einer der größten taxonomischen Gruppenkategorien zur anderen sich ganz genau so verhalten, wie diejenigen von körperlichen Merkmalen. Mit anderen Worten, diese Bewegungsweisen sind ebenso verläßliche Charaktere der betreffenden Gruppen, wie die Form von Zähnen, Federn und anderen, in der vergleichenden Morphologie verwendeten und bewährten Kennzeichen. Für diese Tatsache gibt es keine andere Erklärung, als daß die Ähnlichkeiten und Unähnlichkeiten dieser Bewegungskoordinationen auf die gemeinsame Abstammung von einer Ahnenform zurückzuführen sind, der diese Bewegungen in einer Urform ebenfalls schon zu eigen waren. Kurz, der Begriff der Homologie ist auf sie anwendbar.

In seiner Arbeit „Über bestimmte Bewegungsweisen der Wirbeltiere“ (1930) hat HEINROTH diesen Gesichtspunkt auf weit größere Gruppenkategorien ausgedehnt und gezeigt, daß der taxonomische Wert einer Bewegungsweise, wie z. B. das Kratzen des Kopfes mit dem Hinterfuß, wie wir es alle vom Hund kennen, der gleiche ist wie der der allerältesten morphologischen Merkmale des Kladus, etwa des Aufbaues der Hinterextremität aus Femur, Tibia und Fibula. Das besondere Verhalten dieses Bewegungsmerkmales innerhalb der Klasse der Vögel zeigt, daß die Einzelheiten der Bewegung ausschließlich von historischen und überhaupt nicht von funktionellen Momenten bestimmt werden. Ein Großteil der Vögel führt die Kratzbewegung in der Amphibien, Reptilien und Säugern eigenen Weise so aus, daß der kratzende Hinterfuß lateral an der Vorderextremität vorbei kopfwärts wandert, der Flügel also in die den Vierfüßlern eigene Lage zurückgebracht werden muß, ehe die Bewegung ablaufen kann. Dieses historisch aus dem – sit venia verbo – Klassenwandel des Reptilienarmes verständliche Vorgehen wurde nun im Laufe der Phylogenese von einzelnen Gruppen verlassen, zugunsten der funktionell selbstverständlichen Methode, den ohnehin dem kratzenden Fuß nicht im Wege stehenden Flügel ruhig auf dem Rücken zu belassen und sich „vorneherum“ zu kratzen. Die Verteilung des Vorne- und Hintenherum-Kratzens im System zeigt überhaupt keine Beziehungen zu funktionellen Momenten, Lang- oder Kurzbeinigkeit, Fußform und dergleichen, sondern richtet sich ausschließlich nach der Gruppenzugehörigkeit. *Chionis* dokumentiert seine rätselvolle und isolierte systematische Stellung dadurch, daß er ein Intermedium zwischen Vorne- und Hintenherum-Kratzen ausführt, indem er den Fuß medial am Flügel vorbei zum Kopfe führt, ein an sich nur historisch verständliches Verhalten. Andere Bewegungsweisen, wie das Gähnen, das Sich-Strecken, Sich-Schütteln u. a., zeigen eine ähnlich weite Verbreitung im System.

Neben dieser, einzelne Merkmale sozusagen durch ihre ganze stammesgeschichtliche Entwicklung verfolgende Arbeit hat HEINROTH auch den zweiten Weg vergleichender Forschung in die Verhaltenslehre getragen und, wie WHITMAN, aber in noch tiefgreifenderer Weise, eine beschränkte Tiergruppe auf Grund breitesten Beobachtungsmaterials in allen ihren systematisch verwertbaren Verhaltensmerkmalen bearbeitet, und zwar die Anatiden. Die taxonomischen Schlüsse HEINROTHS (1910) haben eine eindrucksvolle Bestätigung durch die Untersuchungen von POLL (1910) erfahren, der den Grad der

Unfruchtbarkeit von Mischlingen zum Maß stammesgeschichtlicher Verwandtschaft machte: In allen Fällen, in denen beide Forscher von der herkömmlichen Einteilung der Gruppe abwichen, stimmten sie untereinander überein.

HEINROTH hat nie den Ausdruck Homologie gebraucht, noch hat er den Begriff des Instinktes näher definiert oder eine physiologische Erklärung der vergleichbaren Bewegungsweisen angestrebt. Aber mit dem feinen systematischen Taktgefühl des begnadeten Taxonomen hat er eine wesentliche Eigenschaft jener physiologischen Mechanismen gesehen, die wir heute als Instinktbewegungen bezeichnen. Wie wir heute mit ziemlicher Sicherheit wissen, beruhen diese nicht auf Verkettungen polysynaptischer Reflexe, sondern auf jenen Vorgängen endogener Reizerzeugung und zentraler Koordination, deren Kenntnis wir im wesentlichen ERICH VON HOLST verdanken. Die Formkonstanz und Unveränderlichkeit durch äußere Reize, die für die zentralkoordinierte Bewegung so kennzeichnend ist, macht sie begreiflicherweise der deskriptiven Forschung besonders gut zugänglich und fordert geradezu die vergleichende Betrachtung heraus. Man kann von einer Morphologie des Verhaltens sprechen.

Es ist geistesgeschichtlich von großem Interesse, daß OSKAR HEINROTH im Laufe morphologischer und taxonomischer Forschung zu der Entdeckung homologisierbarer Bewegungsweisen kam. HEINROTH strebte im Grunde nach einer Feinsystematik der Anatiden. Für die Beurteilung verwandtschaftlicher Zusammenhänge ist es notwendig, Homologien und Analogien streng zu unterscheiden, mit anderen Worten, Ähnlichkeiten, die auf Stammesverwandtschaft beruhen, nicht mit solchen zu verwechseln, die durch konvergente Anpassung verursacht sind. Das sicherste, merkwürdigerweise selten erwähnte Mittel, diese Unterscheidung zu treffen, ist eine Wahrscheinlichkeitsbetrachtung. Ein Delphin und ein Ichthyosaurus sind einander in der Körperform und in der Ausbildung der Bewegungsorgane und in wenigen weiteren Merkmalen ähnlich, in tausenden von Merkmalen aber ist der erste ein Säugetier, der zweite ein Reptil. Wollte man die Ähnlichkeiten beider Tierformen aus ihrer Abstammung von einem gemeinsamen Ahnen erklären, müßte man die vielen, vielen Merkmale, die der Ichthyosaurier mit Reptilien und der Delphin mit den Säugern gemein hat, ihrerseits auf konvergente Anpassung zurückführen können, was offensichtlich unmöglich ist.

Je näher zwei Tierformen verwandt sind, die einander durch konvergente Anpassung noch ähnlicher wurden, desto mehr verliert diese Wahrscheinlichkeitsrechnung an Sicherheit. Die Merkmale, die eine so kleine Gruppe, wie etwa die bussardähnlichen und die habichtähnlichen Raubvögel voneinander unterscheiden, sind nur um wenig zahlreicher als diejenigen, die durch konvergente Anpassung entstanden, als sich aus beiden Gruppen Großraubvögel, sogenannte Adler, entwickelten. Die älteren Ornithologen betrachteten ganz selbstverständlich alle Raubvogelarten (Raptores), die eine bestimmte Mindestgröße überschritten, als ,,Adler", weil diese Großraubvögel in paralleler Anpassung an das Schlagen verhältnismäßig große Beutetiere eine Reihe gemeinsamer Merkmale entwickelt haben. Alle haben einen großen Kopf mit grobem Schnabel, große durch Knochenleisten überdachte und so geschützte Augen, was einen entschlossenen und finsteren Blick vortäuscht, sie haben verhältnismäßig dicke, kurzläufige Beine mit starken Zehen und Krallen, alle haben einen verhältnismäßig kurzen Schwanz und breite Flügel, was mit den flugtechnischen Erfordernissen des Stoßens und des Wegtragens schwerer Beute zusammenhängt. Selbst in der neuen ,,Tierenzyklopädie" der Urania werden die Adler als eine

Verwandtschaftsgruppe behandelt. In Wirklichkeit sind es mindestens drei Familien von Raubvögeln, aus denen „Adler“ hervorgegangen sind, erstens die Bussarde (Buteonini), zu denen Steinadler, Kaiseradler, Zwergadler und andere gehören, zweitens die Milane (Milvini), zu denen alle Formen der Seeadler (*Haliaeetus*) und andere gehören, und drittens die Habichte (Accipitrini), zu denen Habichtsadler, Kampfadler, Affenadler und andere zu zählen sind. Wenn man alle erreichbaren „kleineren Merkmale“, vor allem auch solche des Verhaltens, mit verwertet, kann man an dieser Zugehörigkeit der Adler zu drei verschiedenen Gruppen kaum zweifeln. Alle Tiergärtner und Falkner, die ich befragte, weil sie Kenner der in Rede stehenden Vögel waren, betrachteten die hier skizzierte Zuordnung als eine Selbstverständlickeit. Die Museums-Taxonomen, die „Balgforscher“, die der alte Alfred Edmund Brehm so sehr verachtete, neigen dazu, Knochenstrukturen, vor allem solche, die man messen kann, für die wichtigsten aller Merkmale zu halten. Erwin Stresemann pflegte in seiner sarkastischen Art zu sagen, daß diese Leute meinten, jene Merkmale, die im Museum den Angriffen der Motten und des Kabinettkäfers *Anthrenus* am längsten Widerstand leisteten, seien auch in der Stammesgeschichte am schwersten veränderlich. Die Schädel von Adlern der verschiedensten Gruppenzugehörigkeit sind einander in der Tat zum Verwechseln ähnlich, aber gerade „die Schädelknochen sind Wachs in den Händen der Evolution“ – wiederum ein Zitat von Stresemann.

Will man das, was die Intuition, das „systematische Taktgefühl“ dem Forscher eingibt, rational nachweisen, so hat man keinen anderen Weg, als zu versuchen, alle jene vielen Merkmale herauszufinden, die in den großartigen Verrechnungsapparat der menschlichen Gestaltwahrnehmung eingegangen sind, denn dieser ist es, dessen Leistungen wir untersuchen müssen. Dieser Verrechnungsapparat ist zwar höchst kompliziert und wunderbar, aber keineswegs ein Wunder! Wir müssen also herausfinden, welche Merkmale der Steinadler mit den Bussarden, der Seeadler mit den Milanen und die Harpyie mit den Habichten gemeinsam haben. Dies müssen Merkmale sein, die jeder der betreffenden Gruppen ausschließlich zu eigen sind, nicht etwa allgemeine Merkmale einer weiteren taxonomischen Einheit, anderenfalls würden sie ja nicht für die spezielle Verwandtschaft sprechen. Man muß imstande sein zu zeigen, daß nicht etwa schon eine Stammesgruppe, von der alle „Adler“ herstammen, diese Merkmale besaß. Nur diese dürfen mit jenen quantitativ verglichen werden, die bei diesen Großraubvögeln sicher durch konvergente Anpassung entstanden sind. Bei dieser quantitativen Einschätzung der analogen Merkmale erhebt sich noch die schwierige Frage, was denn eigentlich als „ein“ Merkmal gezählt werden darf. Es gibt scheinbar voneinander unabhängige Merkmale, ja oft solche verschiedener Organe, die immer nur zusammen auftreten und daher eigentlich als nur ein einziges Merkmal gezählt werden dürfen. Extreme Stromlinienform und sichelförmige Flügel oder Flossen bei Vögeln, Walen und Haien sind z. B. genau genommen nur ein Merkmal.

Je näher die Ausgangspunkte der Konvergenz, desto weniger an der Zahl sind naturgemäß die gruppenspezifischen und sicher homologisierbaren Merkmale. Während bei den erwähnten Raubvögeln der Nachweis der Gruppenzugehörigkeit immerhin noch möglich ist, erweist er sich in anderen Fällen nahezu unmöglich. Es gibt in Abessinien einen zu den Brandentenartigen (Tadornini) gehörigen Schwimmvogel, die Blauflügelgans *Cyanochen cyanopterum*. Sie ist einer der vielen Anatiden, die in Anpassung an das Grasfressen einen gänseähnlichen Schnabel entwickelt haben. Nun gibt es in Südamerika

die sehr artenreiche Gattung *Chloephaga*, die auch zu den Tadornini gehört und einen Gänseschnabel besitzt. Man weiß nicht, ob *Cyanochen* von einigen zufällig einmal von Südamerika nach Afrika verschlagenen *Chloephaga* abstammt, oder ob sie ihre Gänsemerkmale konvergent und unabhängig in ihrer jetzigen Heimat entwickelt hat. Bisher hat sich noch niemand die Mühe gemacht, in Anatomie und Verhalten von *Cyanochen* gezielt nach gruppen-spezifischen *Chloephaga*-Merkmalen zu suchen, vielleicht könnte eine solche Suche die obige Frage entscheiden.

Es ist nicht nur die Verhältniszahl homologer und analoger Merkmale für die Beurteilung von Verwandtschaftsverhältnissen maßgebend, sondern außerdem noch ein Wissen um die Geschwindigkeit, mit der sich einzelne Merkmale bei einzelnen taxonomischen Gruppen verändern. Dasselbe Merkmal kann bei einer Tiergruppe ungemein konservativ, d. h. bei allen Mitgliedern ähnlich ausgebildet sein, während es bei einer anderen Gruppe von Art zu Art sehr verschieden ist, d. h. also phylogenetisch sehr rasch veränderlich. Bei den allermeisten Tetrapoden ist die Vierbeinigkeit ein recht konservatives Merkmal, aber in einigen Teilgruppen, beispielweise bei den Skinken (Scincidae) gibt es nahe Verwandte, von denen die einen vierbeinig, die anderen zweibeinig und die dritten beinlos sind. Bei den Papageien (Psittaci) ist die Gefiederfärbung häufig auch bei ganz nahe verwandten Formen völlig verschieden, während die Schnabelform und -funktion bei allen Mitgliedern der Ordnung nahezu dieselbe bleibt. Bei den Galapagos-Finken (Geospizidae), sowie bei den hawaiischen Kleidervögeln (Drepanidae) ist das genau umgekehrt, die Gefiederfärbung jeder dieser Gruppen ist sehr einheitlich, während die Schnabelform außerordentlich veränderlich ist. Es gibt kein einziges Merkmal, dem man vorwegnehmend eine konstante Bedeutung zumessen kann, die in verschiedenen Tiergruppen gleich bewertet werden darf.

Hans Gadow hat in seiner Bearbeitung der Vögel in ,,Bronns Klassen und Ordnungen des Tierreiches" ein interessantes Gedankenexperiment gemacht, indem er nach 30 anerkanntermaßen gewichtigen Merkmalen eine taxonomische Einteilung der Klasse vornahm, dabei aber jedem der Merkmale die gleiche ,,taxonomische Dignität" zuerkannte. Die so entstehende Taxonomie der Vögel zeigte neben manchen klaren Übereinstimmungen mit der Anordnung, die jedem Taxonomen selbstverständlich ist, auch eine Reihe völlig abstruser Abweichungen. Gadow erkannte richtig, daß die Intuition des begabten Zoologen eine sehr viel größere Anzahl von Merkmalen verwertet als nur dreißig.

Wie aus diesen Erwägungen hervorgeht, beruhen unsere Aussagen über Stammesverwandtschaft verschiedener Lebewesen auf Wahrscheinlichkeitsbetrachtung, und die Wahrscheinlichkeit ihrer Richtigkeit steigt mit der Zahl der verwerteten Merkmale wie auch mit der der Merkmalträger. Daher ist unsere Rekonstruktion der großen Äste des Tierstammbaumes mit einer an Sicherheit grenzenden Wahrscheinlichkeit richtig. Dagegen werden unsere Aussagen umso weniger sicher, je mehr unsere Untersuchung sich mit den feineren, jüngeren Verästelungen dieses wunderbaren Gewächses beschäftigt. Dazu fällt in diesem Falle die Bestätigung durch die Palaeontologie fort.

Diese Unsicherheit bildete ein Hindernis für einen der wichtigsten Durchbrüche moderner Naturwissenschaft, nämlich für die Synthese von Phylogenetik und Genetik. Nur subtilste Massenkenntnis von Merkmalen und Tierformen konnte die Grundlage für den Brückenschlag zwischen Stammesgeschichts- und Erbforschung abgeben. Selbst in der Ornithologie erregte, wie Erwin Stresemann erzählt, ein Mann wie Ernst Hartert den Spott der Fachgenossen dadurch, daß er ,,auf die allersubtilste Unterscheidung lokaler

Formen " drang und dies schon 1899 mit der Behauptung begründete: ,,Schwer unterscheidbare Formen müssen beobachtet werden, da sie in der Natür vorkommen (und wir keine Erscheinungen beim Studium der Natur unberücksichtigt lassen dürfen)." Man möchte meinen, daß der große Systematiker intuitiv geahnt hat, daß das Studium gerade dieser nur fälschlich als Kleinigkeiten betrachteten Einzelheiten für wichtigste Probleme der Evolution aufschlußreich sein werde. Es ist ein bedauerliches Fehlurteil, den Forscher, der in eine bestimmte, oft eng begrenzte Verwandtschaftsgruppe von Tieren vernarrt zu sein scheint, darob zu verlachen, daß er bei Cladoceren die einzelnen Borsten an den Beinchen zählt, oder bei winzigen Fliegen die Äderchen an den Flügeln.

Nicht nur der große Brückenschlag von der Stammesgeschichtsforschung zur Erblehre ist der geduldigen Merkmalssuche der Feinsystematiker zu danken. Als einen Seitenzweig, der in ganz unerwarteter Richtung zu wachsen bestimmt war, hat die Feinsystematik auch die vergleichende Verhaltensforschung in die Welt gesetzt: Die Entdeckung der Homologisierbarkeit von Bewegungsweisen, die man mit der Entstehung der vergleichenden Verhaltensforschung gleichsetzen darf, wurde von Feinsystematikern gemacht, die unersättlich nach neuen und immer neuen Merkmalen suchten und dabei schließlich dahinterkamen, daß man auch Verhaltensweisen als solche Merkmale benützen kann und zwar als höchst verläßliche. Es ist durchaus kein Zufall, daß es Ornithologen und Vogel-Liebhaber waren, die diese Entdeckung machten. Der Insektenliebhaber freut sich nicht nur am lebenden, sondern auch am wohlpräparierten toten Objekt. Zum Vogel-Liebhaber aber gehört es unbedingt, daß er lebende Vögel beobachtet, seien es freilebende oder gefangengehaltene. Die Sammelleidenschaft des Liebhabers spielt dabei ihre Rolle: Oskar Heinroth hatte die reiche Anatiden-Sammlung des Berliner Zoologischen Gartens zu seiner Verfügung, Whitman sammelte Taubenarten, die er in vielen Flugkäfigen hielt.

In meiner Darstellung der Verdienste Heinroths um die vergleichende Verhaltensforschung habe ich bisher im wesentlichen das wiederholt, was ich in der historischen Einleitung zu meinem neuen Lehrbuch der vergleichenden Verhaltensforschung gesagt habe. Ich könnte nun sehr wohl weiter über die historische Entwicklung der Ethologie sprechen, ich könnte z. B. zeigen, in welcher Weise Oskar Heinroths Fassung des Begriffes von der ,,arteigenen Triebhandlung" zur weiteren Analyse angeregt und entscheidende Fortschritte unseres Forschungszweiges bewirkt hat.

Ich will indessen lieber darüber sprechen, in welcher Weise die Methoden Oskar Heinroths beispielgebend gewirkt haben. Man kann sich keinen überzeugenderen Tribut für die Größe dieses Mannes denken, als die Tatsache, daß wir heute noch in unserer Forschung bis ins kleinste so vorgehen, wie er es tat.

Die eine große Lehre, die wir ihm verdanken, ist ein Erbe der Feinsystematik: Keine Einzelheit, die als konstantes Merkmal einer Art oder einer Unterart beschrieben werden kann, darf vernachlässigt werden. Der schon zitierte Satz Ernst Harterts, daß wir ,,keine Erscheinungen beim Studium der Natur unberücksichtigt lassen dürfen", gilt auch für die Verhaltensforschung uneingeschränkt. Dieser Lehre zu folgen wird einem heute oft dadurch erschwert, daß es kaum noch wissenschaftliche Zeitschriften gibt, die bereit sind, solche Details ernst zu nehmen und zu veröffentlichen. Der Irrglaube, daß die Quantifikation die einzig legitime kognitive Leistung des Menschen sei, kriecht unvermerkt selbst in die Ornithologie.

Die schon besprochenen Eigenschaften der Gestaltwahrnehmung machen es verständlich, daß die Zahl der Daten, die in ihren wunderbaren Verrechnungsapparat eingegeben werden muß, gar nicht groß genug sein kann. Man muß dasselbe Verhaltensmuster wieder, wieder und noch einmal beobachten, dann löst sich auf einmal die ihm innewohnende Gesetzlichkeit vom Hintergrunde des Zufälligen und tritt dem Forscher als ein qualitativ unverwechselbares Erlebnis entgegen. Man empfindet dann stets eine gewisse Verwunderung darüber, daß man etwas so Offensichtliches nicht schon sehr viel früher gesehen hat. Der große Verrechnungsapparat muß ein geradezu gewaltiges Datenmaterial sammeln und speichern, um die gestaltete Wahrnehmung der Gesetzlichkeit vom Hintergrunde des Akzidentellen abheben zu können. Um diese Voraussetzung zu schaffen, ist eine ebenso gewaltige Zeit vonnöten, die in voraussetzungsloser Beobachtung verbracht wird. Selbst ein in asiatischen Geduldsübungen geschulter Heiliger wäre kaum imstande, ohne Nachlassen der Aufmerksamkeit so lange in ein Aquarium oder auf einen Ententeich zu starren wie nötig ist, um die Datenbasis zu schaffen. Dies bringen nur Menschen zustande, deren Blick durch eine völlig irrationale Freude an das Objekt ihrer Forschung gefesselt bleibt. Hierin liegt das Verdienst der Liebhaberei; es ist einer der größten Denkfehler, in dem Ausdruck „scientia amabilis“ ein abwertendes Urteil zu sehen.

Wir haben von HEINROTH gelernt, daß man ein Tier gar nicht lange genug anschauen kann und daß man, wenn irgend möglich, mit ihm leben muß, um jenen Grad intimer Tierkenntnis zu erwerben, der die Voraussetzung erfolgreicher Verhaltensforschung ist.

Ein zweiter Punkt, in dem wir der Methodik HEINROTHS aufs Genaueste folgen, betrifft das Studium der Ontogenese des Verhaltens. Wir untersuchen das Verhalten einer Tierart, wo das nur irgend möglich ist, „vom Eierschlupf bis zum Todeshupf“, wie HEINROTH selbst sagte. Wenn man das Verhalten einer Art nur von erwachsenen Individuen kennt, und sei es noch so gründlich, und anschließend ein kleines Junges großzieht, ist man immer wieder erstaunt über die Menge des Wissenszuwachses, den dieses Verfahren liefert.

Die dritte methodische Lehre OSKAR HEINROTHS, die wir aufs Genaueste befolgen, ist die Ausschöpfung einer Wissensquelle, die nur dem Beobachter gefangener Tiere zugänglich ist: Störungen des Verhaltens, die durch die Gefangenschaftsbedingungen entstanden sind, können uns Wesentliches über die normale Physiologie des gestörten Verhaltensmechanismus sagen.

Wenn ein Freilandbeobachter zu sehen bekommt, wie ein Wolf einen Beuterest eingräbt, so ist der Arterhaltungswert der Verhaltensweise selbstverständlich, die Frage nach ihrem kausalen Zustandekommen bleibt unbeantwortet. Wenn jemand dagegen sieht, wie der zahme junge Wolf einen Knochen in die Zimmerecke trägt, hinlegt, dicht daneben scharrt, den Knochen mit der Nase an die Stelle des Scharrens schiebt und anschließend mit der Nase nicht vorhandene Erde auf das nicht gegrabene Losch schaufelt, so hat man Wichtiges über das stammesgeschichtlich entstandene Programm des Verhaltensmusters erfahren.

Verwandt mit dieser Wissensquelle ist die Beobachtung pathologischer Störungen des Verhaltens. Die Pathologie, die absichtliche, experimentell gesetzte Störung, ist bekanntlich eine der wichtigsten Wissensquellen der Physiologie; oft ist der Forscher erst durch den Ausfall eines bestimmten Mechanismus auf dessen Existenz aufmerksam gemacht worden. Auch pathologische Störungen des Verhaltens können uns Wichtiges lehren. Der

Intensitätsschwund bestimmter Instinktbewegungen, der bei gefangenen Tieren nur allzu leicht auftritt, hat Heinroth und mich als erstes darauf aufmerksam gemacht, daß das Tier als Subjekt keine Ahnung vom dem arterhaltenden Sinn seiner angeborenen Verhaltensmuster hat: Es kommt bei gefangenen Tieren ungemein oft vor, daß sie wegen Mangels ausreichender Intensität einen Verhaltensablauf genau dann abbrechen, wenn sein arterhaltender Sinn beinahe erfüllt ist. Beobachtungen dieser Art waren es auch, die mich erstmalig auf die Unsinnigkeit der Annahme eines untrüglichen Instinktes aufmerksam machten. Ich möchte gerade diese Wissensquelle besonders hoch einschätzen. Es ist sicher kein Zufall, daß Heinroth Mediziner war.

Schließlich sei noch eine Methode Heinroths erwähnt, die wir von ihm gelernt haben und die in meinem eigenen kleinen Institut eine wichtige Rolle spielt, das ist die Haltung zahmer Tiere in völliger Freiheit. In meiner persönlichen wissenschaftlichen Entwicklung hat es eine entscheidende Rolle gespielt, daß meine erste jung aufgezogene Dohle gerade in jener Woche flügge wurde, als mir die Lieferung der ,,Vögel Mitteleuropas" ins Haus kam, in der Heinroth über den Freiflug seiner Kolkraben berichtet. So entstand meine Erstlingsarbeit ,,Beobachtungen an Dohlen" (Journ. f. Ornithol., 1927). Heinroth und Stresemann hatten mich dann energisch ermutigt, die Beobachtungen an freifliegenden zahmen Dohlen fortzusetzen, was geradezu zu einer ,,Weichenstellung" für mein ganzes späteres Leben geworden ist.

Die Methode, jung aufgezogene zahme Tiere in völliger Freiheit und möglichst natürlichem Biotop zu studieren, hat die Wahl der wichtigsten Objekte unserer Forschungen bestimmt. Die Vorteile dieser Untersuchungsmethoden liegen auf der Hand, ihre Grenzen sind durch die Eigenschaften des sogenannten Prägungsvorganges gezogen, der vor allem bei Vögeln eine wichtige Rolle spielt. Bei Rabenvögeln, Papageien, Reihern und anderen ist es schwierig, die Vögel so aufzuziehen, daß sie zwar in ihren Kindestriebhandlungen und ihrer sozialen Anhänglichkeit auf den Menschen fixiert werden, nicht aber in Bezug auf die Verhaltensweisen der Sexualität und des Rivalenkampfes. Ein großer Gelbhaubenkakadu oder ein männlicher Kolkrabe kann alle weitere Beobachtungen vereiteln, wenn er den Pfleger als Rivalen behandelt. Gänse der verschiedensten Arten sind deshalb für die in Rede stehende Untersuchungsweise so gut geeignet, weil die auf das Elterntier und den sozialen Kumpan gerichteten Verhaltensweisen leicht und nachhaltig auf den menschlichen Pfleger fixiert werden können, eine sexuelle Prägung auf den Menschen aber bei diesen Vögeln nahezu unmöglich ist.

Versucht man, zu Beobachtungszwecken eine Population zahmer und freilebender Tiere anzusiedeln oder einer natürlichen Population zahm aufgezogene Individuen einzugliedern, so stößt man manchmal, besonders bei den höchstentwickelten Säugetieren, auf eine unerwartete Schwierigkeit. Auch wenn sie mit Erfolg in den Lebensraum eingewöhnt werden, der dem natürlichen weitgehend entspricht, bilden die vom Menschen aufgezogenen Tiere nicht die für ihre Art typische Form der Sozietät. Amerikanische Versuche, in weiten Gehegen Schimpansen anzusiedeln, die als ausgediente Versuchstiere das Gnadenbrot verdient hatten, scheiterten völlig. Katharina Heinroth berichtet anschaulich ihre vergeblichen Versuche, handaufgezogene junge Paviane in die Horde gleichartiger Tiere einzugliedern, die den großen Affenfelsen des Berliner Zoologischen Gartens bewohnten. Die vom Menschen aufgezogenen Individuen erregten immer wieder den höchsten Zorn ihrer Artgenossen durch Verhaltensweisen, die nicht ,,sozietätsgemäß" waren, ,,sie

benahmen sich daneben", wie Frau HEINROTH sich ausdrückte. Diese Unstimmigkeiten sind deshalb bedeutsam, weil sie auf das Vorhandensein traditioneller Verkehrsnormen schließen lassen.

Bei handaufgezogenen Wildschweinen besteht die eben beschriebene Schwierigkeit nicht, offenbar ist hier das ganze Inventar sozialer Interaktionen genetisch festgelegt und bedarf keiner Ergänzung durch soziale Tradition. Gerade diese Schwierigkeit in der Haltung und Beobachtung zahmer, freilebender Tiere weist auf ein Problem hin, das nur durch den Vergleich zwischen menschenaufgezogenen und natürlichen Populationen untersucht werden kann.

Das methodische Ideal der Beobachtung hochorganisierter Lebewesen ist dann erreicht, wenn es gelingt, freilebende Tiere so an den Beobachter zu gewöhnen, daß ihr Verhalten durch seine Gegenwart nicht verändert wird, ja, daß er sogar mit ihnen in natürlicher Umgebung Experimente anstellen kann. Vor allem in der Erforschung von Primaten ist diese Methode von Wichtigkeit, da bei ihnen soziale Tradition eine sehr große Rolle spielt, so daß bei freigelassenen, aus der Gefangenschaft stammenden zahmen Tieren ein artgemäßes Sozialverhalten nicht zu erwarten ist. Die Schimpansenbeobachtungen JANE GOODALS haben denn auch die gebührende Beachtung gefunden. Die Pavian-Beobachtungen von WASHBURN, DE VORE und vor allem die Studien von HANS KUMMER zeigen, wie sehr diese äußerst zeitraubende und so manche Opfer fordernde Methode durch ihre Ergebnisse lohnt.

OSKAR HEINROTH betrachtete Tierkenntnis als die Grundlage aller Verhaltensforschung. Er war Tierkenner katexochen, er betrachtete das Beobachten und Festhalten kleinster Einzelheiten als die oberste Pflicht des Forschers, er erfüllte hierin die schon zitierte Forderung ERNST HARTERTS mit peinlichster Gewissenhaftigkeit. Im Max-Planck-Institut für Verhaltensphysiologie haben ERICH VON HOLST und ich es ebenso ernst mit dieser Pflicht gehalten. Als ERICH VON HOLST seine klassischen Versuche mit elektrischer Reizung des Hypothalamus an Hühnern vornahm, betonte er immer wieder, daß diese Untersuchung ohne genaueste Kenntnis des gesamten Verhaltensinventars der untersuchten Art jeder Grundlage entbehre. Er gewann daher ERICH BAEUMER zum Mitarbeiter, der, von Beruf Landarzt, aus „Liebhaberei" eine profunde Kenntnis des Verhaltens aller Haushuhnrassen gewonnen hatte und daher die für VON HOLSTS Versuche unentbehrliche Fähigkeit besaß, auch bei geringsten Andeutungen und Bruchstücken bestimmter Verhaltensmuster eine exakte Diagnose stellen zu können. Aus gleichen Gründen hat seinerzeit W. R. HESS zur Auswertung seiner Filme von den Versuchen der Stammhirn-Reizung an Katzen die Mitarbeit PAUL LEYHAUSENS beansprucht, der das gesamte Verhaltensinventar dieser Tiere, das noch wesentlich komplexer ist als das des Haushuhns, „am Schnürchen" hat. Ohne diese Voraussetzung sind Stammhirn-Reizversuche meines Erachtens sinnlos.

Ich möchte die Frage aufwerfen, ob dies nicht für alle Untersuchungen tierischen Verhaltens schlechthin gilt. Selbst wenn man bewußt das Forschungsinteresse auf ein sehr kleines Untersystem der Ganzheit beschränkt, ist, so will mir scheinen, die Kenntnis des ganzen Verhaltensinventars der untersuchten Tierart unumgänglich nötig. Ohne sie weiß der Untersucher ja gar nicht, was nun eigentlich die Antwort sei, mit der das System auf seine Maßnahmen, welche immer das sein mögen, reagiert.

Schon um zu wissen, ob eine beobachtete Verhaltensweise dem artgemäßen Verhalten in freier Natur entspricht, oder ob sie pathologisch sei, muß der Untersucher seine Tierart

sehr genau kennen. Unzählige Irrtümer beruhen darauf, daß der pathologische Intensitäts-Verlust oder das völlige Schwinden zentralkoordinierter Bewegungsweisen für „normal" angesehen wurden. Zur Tierkenntnis als Forschungsmethode gehört auch ein gewisses Maß an „klinischem Blick", den man nur in langer Erfahrung zu erwerben vermag. Ich werfe einem sehr großen Teil der jüngeren Forscher, die sich selbst für Ethologen halten, einen bedauerlichen Mangel an Tierkenntnis und klinischem Blick vor.

OSKAR HEINROTH ist der Prototyp des induktiven Naturforschers gewesen. Er hat immer die Induktionsbasis für wichtiger gehalten als alle Gebäude noch so scharfsinniger Schlußfolgerungen, die sich auf dieser Grundlage erheben. Er hat TINBERGEN und meinen theoretischen Folgerungen immer etwas zögernd recht gegeben.: „Ja, ja, das ist schon richtig, aber so möchte ich es doch eigentlich nicht sagen." Sehr oft hat er Theorien, die in einzelnen Punkten falsch waren, durch Gegenbeispiele widerlegt, sein Allgemeinwissen über tierisches Verhalten war enzyklopädisch. Wenn ich einige Zeit mit HEINROTH verbracht hatte, schied ich nie von ihm, ohne irgendetwas Tatsächliches von ihm gelernt zu haben, was von unvergeßlichem Werte war. Wenn ich daran denke, kann ich mich nicht eines großen Bedauerns enthalten über die ungeheure Menge des Wissens, die dieser Mann mit ins Grab genommen hat.

HEINROTH liebte es, sich ein wenig zynisch zu geben, besonders wenn sich die Möglichkeit bot, spießbürgerliche Menschen ein wenig zu schockieren. In Wirklichkeit war er das Gegenteil von einem Zyniker. Er stand den großen Wundern der Natur mit aller gebührenden Ehrfurcht gegenüber, vor allem dem schöpferischen Geschehen der Evolution. Er konnte ernstlich böse werden, wenn er hörte, wie Besucher des Aquariums oder des Zoos über ein Tier lachten, das, wie ein Ameisenbär, ein Chamäleon oder ein Anglerfisch durch die bizarren Formen seiner extremen Anpassung die Heiterkeit der Besucher erregte. Ich habe ihn bei einer solchen Gelegenheit sagen hören: „Der lacht doch gerade über das, was für unsereinen der liebe Gott ist."



Problems of the Classification of Birds, a Progress Report. Erwin Stresemann Memorial Lecture

Ernst Mayr

It would be unthinkable to hold an International Ornithological Congress in Berlin without paying tribute to the memory of that great man who for 50 years dominated the intellectual life of German and, indeed, of World ornithology. When Stresemann celebrated his 80th birthday, I had the honor to present him, on behalf of the Deutsche Ornithologen Gesellschaft, a congratulatory message. May I be permitted to quote a few sentences from this message, because they express my evaluation of his achievements in a manner, on which I can hardly improve.

Lieber Freund,

Trotz aller Betonung der Freiheit wissenschaftlicher Forschung bedarf es der Führer in der Wissenschaft genau wie anderswo. Die Ornithologie war in den 20er Jahren eines solchen Führers dringend bedürftig. In den großen Museen der Welt, in denen die meisten Fachornithologen tätig waren, war die Vogelsystematik zum Selbstzweck geworden. Die Gattungen wurden immer feiner gespalten, bis schließlich fast jede Art ihre eigene Gattung hatte, und die Subspezies wurden einer ähnlichen Pulverisierung unterworfen. Die Verfasser der Lokalfaunen taten es nicht besser, ihr Ideal war es geworden, möglichst viele Raritäten aufzuführen. Die große Linie war völlig verloren gegangen.

Da hast Du Fenster und Türen geöffnet und eine neue Luft durch die Hallen der Ornithologie wehen lassen. Obwohl Du das Journal 1922 unter den schwierigsten Umständen (Nachkriegswirren, Inflation) übernahmst, ist es Dir doch rasch gelungen, es in neue Bahnen zu leiten. Themen aus den Gebieten der Evolution, der Genetik, des Verhaltens fanden plötzlich bereitwillig Zugang zum Journal. Gleichzeitig hast Du am Zoologischen Museum der Universität Berlin eine ornithologische Schule gegründet, die bald einen weltweiten Ruf hatte. In selbstlosester Weise fördertest Du einen Briefwechsel mit jungen Vogelfreunden in allen Teilen Deutschlands und der Welt, und warbst damit viele Mitarbeitern, die ohne deine Ermutigung Dilettanten geblieben wären. In weniger als zehn Jahren hast Du es fertiggebracht, das Journal zur führenden ornithologischen Zeitschrift zu machen. Ja, es entwickelte sich zu einer Zeitschrift, die sich durchaus mit den besten zoologischen Zeitschriften der Welt messen konnte. Das Ideal, das Du der Welt-Ornithologie setztest, hat Ibis, Auk, Condor und Ardea als glückliches Vorbild gedient.

Daß sich für die Ornithologie in den 20er Jahren eine neue Epoche eröffnete, verdankt sie Deinem Schöpfertum und Deiner Schaffenskraft. Aere perennius ist das Denkmal, das Du Dir mit Deinem wissenschaftlichen Lebenswerk gesetzt hast.

And now let us ask, what were Stresemann's contributions to bird taxonomy? The area of avian classification in which Stresemann was most interested and in which he was a master, was the study of species. He realized that the species is the keystone of all

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U. S. A.

biological research and he considered it his major objective, as an avian taxonomist, to clarify the status of the hundreds if not thousands of doubtful nominal species which cluttered up the literature. More clearly than any of his contemporaries, he saw that three quite separate problems had to be solved in order to achieve this task:

(1) First, all sibling species-complexes had to be dissected into the component species;

(2) Second, all morphs (or "Mutationen" as STRESEMANN called them) had to be unmasked and assigned to the populations of which they form part;

(3) and finally, all geographical isolates had to be assigned to the polytypic species to which they belong.

Let me begin with points (1) and (2). In line with his endeavor to straighten out complexes of sibling species, STRESEMANN systematically revised one "difficult" genus after the other, such as *Collocalia, Accipiter, Zosterops, Cyornis, Pericrocotus,* and many others I might care to mention. These revisions were not necessarily the last word, but in each case they converted existing chaos at least into preliminary order. (For a bibliography of these revisions, see Mitt. Zool. Mus. Berlin 46 (1970), p. 7–29, and J.Orn. 114 (1973), 482–500.)

The second area to which STRESEMANN devoted literally scores of publications was the phenomenon he called "Mutationen", in line with the terminology of the early Mendelians, but now called morphs. Again and again STRESEMANN showed that a so-called species of the ornithological literature was nothing but a color variant of another species and could be stricken from the inventory of avian species.

By far the greatest amount of effort and ingenuity, however, STRESEMANN devoted to the correct allocation of geographic isolates. STRESEMANN always considered himself a disciple of ERNST HARTERT and he followed his master in the endeavor to assign all geographic isolates to the polytypic species to which they seemed to belong. In some of his earliest papers he permitted his youthful enthusiasm to carry him too far. For instance, the forms which he combined in 1916 in *Corvus coronoides* we now assign to five good species. At that time STRESEMANN more or less followed the principles of KLEINSCHMIDT according to whom all geographic representatives had to be combined into a single Formenkreis. In the mid-1920's STRESEMANN abandoned this extremism and we find in the J.Orn. for 1927 a rather amusing controversy between STRESEMANN and HARTERT on the question whether the desert horned lark of the Sahara *(Eremophila bilopha)* should, or should not, be included in the Holarctic *Eremophila alpestris,* with STRESEMANN defending the recognition of *bilopha* as a separate species.

More important than such rather technical matters was STRESEMANN's consistent emphasis on the primacy of biological over morphological criteria. In 1919, in his *Certhia* revision, he gave an excellent definition of the biological species. He said (1919:64) that speciation is then completed "when two speciating forms have diverged physiologically from each other to such an extent that they can come together again in nature without interbreeding." And he emphasized that "morphological divergence is independent of physiological divergence" (page 66). At a later period (1943) he was one of the first to stress the fact that speciation affects not only reproductive isolation but also ecological divergence, and that the adaptation of populations to new habitats and ecological niches is often a decisive component in the speciation process.

Again and again Stresemann was pioneering with new taxonomic ideas. He exerted a far reaching influence not only through his philosophy which dominated what was published in the J.Orn. but also through his students like myself and Meise or through his associates at the Berlin Museum like Rensch.

I shall repeatedly come back to Stresemann's ideas but let me now concentrate on the special subject matter of my presentation.

Microtaxonomy

One can distinguish two levels at which activities of classification are performed. Classification at the species level can be referred to as microtaxonomy, and classification at the level of the higher categories as macrotaxonomy. As far as the species level is concerned, it is generally admitted that avian taxonomy is more mature than that of any other group of organisms. Yet, even at this level, complete stability has not yet been achieved as becomes evident when we attempt to answer the question: How many species of birds are there? We then realize that we first have to answer the question: What factors affect the recognition and delimitation of bird species? When we try to answer this question, we discover that there are three sets of such factors and that they are, in part, in conflict with each other.

1. The downgrading of geographical isolates from the rank of species to subspecies in the course of the revision of polytypic species;

2. The discovery of genuinely new species, including the unmasking of previously unrecognized sibling species, also the discovery of geographical overlaps of taxa previously considered subspecies;

3. The recent trend to upgrade highly distinct and geographically isolated subspecies to the rank of allospecies.

Let me now discuss these three sets of causes before coming to a final conclusion. The downgrading of thousands of geographic isolates, originally described as full species, to the rank of subspecies together with their assemblage into polytypic species was one of the major concerns of the New Systematics. Stresemann was one of the leaders in this endeavor. This phase of the new systematics is now virtually completed but a comparison of faunal lists published between the 1930's and 1970's shows how recent much of the work was.

When Peters in 1931 published the first volume of his Checklist of Birds of the World, he presented what he considered a definitive list of species. His expectation, however, was not fulfilled; the changes in the past 48 years are, indeed, quite astounding (Table 1).

The second factor which affects the stability of species classification is the discovery of new species. The question here is: How complete is our inventory of avian species? There is no doubt that an appreciably large number of species was still to be discovered in the 1920's and 1930's. At that time within less than 10 years I myself was able to describe more than 20 new species, all of them from the circumscribed island region east of New Guinea. The law of diminishing returns, however, has asserted itself in the meantime and most young bird taxonomists will never have the opportunity to describe even a new single species. But when will the last bird be discovered?

I'm afraid I have consistently underestimated the number of still undiscovered species. In 1935 (page 22) I predicted "I believe that the number of still undescribed species of birds is below 100." About 140 good new species have already been described since that date. Surely, this is an impressive figure, even though it is only 1.6% of the total of species known in 1935.

TABLE 1. Changes in the inventory of avian species between 1930 and 1978.

Number of species recognized in Volume 1 (1930) of Peters'	853
Number of these "species" since reduced to subspecies or synonyms	101
	752
Number of valid new species since 1930	13
Taxa listed by Peters' as subspecies or synonyms but considered full species in 1978	34
Taxa considered species in 1978	799

More interesting is the question *where* the new species are being discovered. Prior to 1960 more than half of the new species came from the Indo-Australian island region, from Southeast Asia, or from more or less isolated mountain areas in Africa, in other words from the Old World. But the number of such islands and mountains is limited while the unexplored portions of South America, particularly the slopes of the Andes seem inexhaustible. As a result, the percentage of American species among the new species has been steadily increasing (Table 2). Yet, it would seem improbable that an annual rate of more than 3 new species can be continued much longer.

TABLE 2. New species of birds 1938–1975.

Years	1938–1941	1941–1955	1956–1965	1966–1975
Presumably valid new species described	25	36	33	34
No. per year	6.2	2.5	3.3	3.4
Percent New World	44%	47%	52%	56%

The final number of species to be recognized by the ornithologists will far less depend on future new discoveries than on the third of the factors, I have listed above, future changes in the species concept.

The species problem today

It is now evident that the combining of geographical isolates into polytypic species was not the final solution to the species problem in ornithology. As a matter of fact, as in other groups of animals there are two kinds of species problems, the first being the delimitation of taxa and the second being the decision concerning the appropriate rank (species or subspecies) of these taxa. All the cases where we deal with complexes of sibling species such as are found in Europe in the tree creepers, the great titmice, and *Phylloscopus*, or

elsewhere in the world in the genus *Collocalia*, the *Meliphaga analoga* group of honey eaters in New Guinea, and certain tyrant flycatchers *(Empidonax, Elainia, Myiarchus,* etc.), pose a problem of the recognition of species taxa. In these cases field work (the study of vocalization, etc.) may be necessary for a final answer. A typical case is the African genus *Vidua* with exceedingly similar sympatric host races which are considered good species by some authors but not by others. In a case as that of *Vidua* where the males seem to learn the song of the host species, the final decision may be very difficult, and it may be necessary to test specific distinctness through protein analysis or other methods. Nevertheless, when we add up the totality of such difficult sibling species complexes in all orders of birds in all parts of the world, we arrive at an astonishingly small number. In other words, the task of the correct discrimination of species taxa in birds is virtually completed.

The situation is, however, drastically different as far as the decision is concerned, of how to rank these taxa. Let me make this clear by a rapid historical survey. Ever since geographic variation in birds was recognized, and this recognition goes as far back as Pallas at the end of the 18th century, there has been great uncertainty as to how far to go in the inclusion of geographically representative forms in a single species. The American school of Baird, Coues, and Ridgway adopted the principle to include only those forms in polytypic species that intergrade with each other. The German ornithologist Kleinschmidt went to the other extreme by proposing to combine all related species into a single taxon as long as they were more or less representing each other geographically. He called such assemblages Formenkreise, realizing himself that such an aggregate of allopatric populations was far more inclusive than biological species. Nevertheless, he found a number of followers, and for a while even Stresemann combined allopatric species with an impetuous enthusiasm, until he realized that such assemblages of allopatric forms are highly heterogeneous. In view of this situation, Rensch (1928) proposed to recognize two kinds of Formenkreise, those that are composed of genuine geographic races which he called Rassenkreise, and those which also included allopatric species which Rensch called Artenkreise. In order to make Rensch's concepts more accessible internationally, Mayr translated the term Rassenkreise into polytypic species and the term Artenkreise into superspecies (1931). This terminological distinction was important in order to make clear that geographical replacement is not sufficient to prove conspecificity.

At first, this distinction had little influence on taxonomic practice in ornithology and only few authors adopted the superspecies concept. When in doubt, geographically representative forms continued to be called subspecies since this ranking seemed to convey more information. As a consequence, the polytypic species of the period 1920 to about 1955 was very broadly defined. Eventually, however, it was increasingly recognized that it concealed important evolutionary differences to rank all geographical isolates as subspecies, including those for which morphological and other criteria clearly indicated that they had already reached species level. The result has been an ever greater use of the category superspecies in the recent ornithological literature.

The use of the superspecies encouraged raising many geographical isolates, previously called subspecies, to the rank of allospecies, particularly in island regions. However, treating allospecies as equivalent to species that are not members of superspecies, leads to a sharp increase in the number of recognized species, independent of any discovery of

actual new species. Let me give you some examples (based on Vuilleumier, 1976). In the genus *Diglossa,* for instance, Hellmayr (1935) and all subsequent authors recognized 11 species while Vuilleumier raised the total to 17 by recognizing 6 additional allospecies. Similarly, in the genus *Ortalis* some recent authors recognize only 6 species, others 11; in *Penelope* some authors recognize 6 species, others 15 for the same populations. Many birds from the Polynesian Islands, the Solomon Islands, and New Guinea which I treated as subspecies in the 1930's and 1940's, I now consider to be allospecies in more widespread superspecies. In the 1940's, prior to this development, counts of the total number of species of birds in the world fluctuated around 8,600. At that time, even though new species were added at the rate of three to five per year, many isolated forms that had been previously listed as species were reduced at about the same rate to the rank of subspecies and thus, the grand total did not change materially over many years. However, in the most recent count the number of all bird species (by Bock) the total has risen to 9,021 and it may rise to 9,500 when the new criteria for species recognition are consistently applied to all bird faunas of the world.

The recognition of allospecies raises various problems, particularly for zoogeography, as was seen by Rensch at an early stage. When one compares different faunas, it would be quite misleading to give the same weight to allospecies as to genuine species that are not members of superspecies. Many superspecies of New Guinea birds, for instance, have a different allospecies in almost every mountain range (e. g. *Astrapia, Parotia).* Superspecies are particularly widespread in archipelagos, like the West Indies or the Solomon Islands, and when comparing the fauna of such island regions with that of the nearest mainland, the unit of comparison must be the superspecies, or more correctly the new category "zoogeographic species," composed of superspecies and all those isolated species that are not members of superspecies. The importance of this distinction for zoogeographic comparisons can be shown by a few examples. The total number of species breeding in Northern Melanesia is 237. By allowing only one species per superspecies the figure reduces to 187 zoogeographic species, a reduction of 21%. The total number of breeding North American birds is 518 but the number of zoogeographic species is only 471, a reduction of 9,1%. For the world as a whole, I estimate the number of zoogeographic species to be about 7,000 ± 200.

The question has been raised (Vuilleumier, 1976) whether this new development in the ranking of isolated populations has weakened the biological species concept. In my opinion it has not. The biological species concept has validity only in what I have called the "non-dimensional situation," that is where populations are acutally in contact with each other. The allospecies is one of the forms of semi-species, that is of forms that are in the transition from incipient to full species. Since they are geographically isolated from each other, their species status cannot be tested directly but can only be inferred. The biological species concept itself is not weakened by the fact that there are situations in nature where it cannot be tested.

Let me close this part of my discussion by emphasizing two points. The first is that in ornithology the recognition of species taxa and their delimitation has reached great maturity. The addition of a few unrecognized sibling species or undiscovered species will change the total of known bird species by less than one percent. The situation is different with respect to geographical isolates, where we have experienced a quiet revolution during

the last 25 years owing to the application of the superspecies concept. This has necessitated the recognition of an additional category, the zoogeographic species, the use of which facilitates the comparison of different bird faunas.

Let me add a few comments on the categories below and above the species. The subspecies has by the 1970's lost the importance it had when I was a budding ornithologist. I am sure that at the present time more subspecies names are placed in synonymy than new ones proposed.

As far as the genus is concerned, we have left the 1920's far behind, when Mathews (Australia), Austin Roberts (South Africa) and Oberholser (North America) placed just about every good species in a different genus. Professor Bock very kindly has made the latest count of genera available to me. According to the standards of the latest revisions 2,045 genera are now recognized for 9,021 species and allospecies. This makes for an overall average of 4.41 species per genus. With a consistent adoption of superspecies, it miqht seem advisable to broaden to genus concept and to reduce the total number of genera to about 1,750. At the same time this would be in conflict with the function of a stable binomen as an information retrieval device. Time will tell how this conflict will be resolved.

Macrotaxonomy

Let me now turn to macrotaxonomy, the science of classification. It deals with the determination of relationship among families and orders and with converting it into a most useful classification. For a biologist the primary objective of a classification is to provide the foundation for comparative studies and one might even go so far, as was done by Bock (1976:178), to say that the best classification is the one that permits the most useful comparative investigations.

Those who are not personally active in taxonomic research do not appreciate the immense amount of work that is required for the improvement of a classification. Let us say there are 2,000 genera of birds. For each of these genera one must answer numerous questions. First, what species should be included in this genus, second, is the respective genus justified or could it just as well be combined with another genus, third, what other genus is nearest to it, or more broadly spoken, to what family does the genus belong? And finally, into which suborders and orders should these families be combined?

Taxonomic research above the level of the species and particularly above that of the genus was badly neglected during the period of the new systematics, let us say up to the 1950's. Stresemann, for instance, was not particularly interested in this area of taxonomy. Essentially, he simply adopted the classification of Fürbringer. He, who at the level of species and genera was such a lumper, was definitely a splitter at the level of the higher categories. He recognized 51 orders of birds, as against the 27 or 28 orders recognized by most other ornithologists. His attitude about the relationships of these orders was quite agnostic as expressed in his well known statement: "In view of the continuing absence of trustworthy information on the relationship of the higher categories of birds to each other, it becomes strictly a matter of convention how to group them into orders. Science ends where comparative morphology, comparative physiology, comparative ethology have failed us after nearly 200 years of efforts. The rest is silence" (Auk 1959, 76:277–278).

Such pessimism, however, was an extreme and rather isolated attitude among ornithologists. Nevertheless, the backward state of avian classification right up to the 1960's cannot be denied. For instance, there is not a single bird fauna in the world that does not have its share of genera that raise questions. In North America for instance the Dickcissel *(Spiza)*, the Pinon Jay *(Gymnorhinus)*, the Verdin *(Auriparus)*, the Wren tit *(Chamaea)*, the Dipper *(Cinclus)*, the Solitaire *(Myadestes)*, the Phainopepla, the Olive Warbler *(Peucedramus)*, etc.

As far as the New Guinea fauna ist concerned (in part shared with Australia) one might mention the following genera: *Daphoenositta, Drymodes, Eulacestoma, Eupetes, Ifrita, Machaerirhynchus, Melampitta, Oreocharis, Orthonyx, Pachycare, Paramythia, Peltops*, and *Timeliopsis*.

Among Australian genera, one might mention the following: *Artamus, Ashbyia, Atrichornis, Cincloramphus, Cinclosoma, Climacteris, Corcorax, Dasyornis, Ephthianura, Eremiornis, Falcunculus, Grallina, Menura, Neositta, Psophodes*, and *Struthidea*.

In all these cases either the assignment to the family is in doubt or else the placement within a family. All of the 13 genera I have listed are passerine birds. Even more serious is the problem with such isolated genera as those of the whale-headed Stork *(Balaeniceps)* or the Hoatzin *(Opisthocomus)* or of isolated orders like those of the flamingos and tinamous, the placement of which is still quite controversial. We will never attain a perfect classification of birds until all these genera and isolated families and orders througout the world have been properly assigned to their right places. Since there are numerous such genera in the tropics of Asia, Africa and South America, there is still a very large task ahead of us.

How uncertain the classification of birds is, is perhaps best illustrated by pointing out that there is no certainty for most of the 28 orders of birds, now usually recognized, which other order is its nearest relative. Let us take the Passeriformes for which some authors postulate that they were derived from the Piciformes, others from the Apodiformes, and still others from the Coraciiformes.

As I said, during the flowering of the new systematics, let us say from the 1920's to the 1950's, classification studies were, for a number of reasons, badly neglected. But the situation has now changed. I entirely agree with Bock (1975:176) who said at Canberra: "... the past 25 years have been, without doubt, the most active period in the history of avian classification." This is even more true in 1978 as documented by the symposia and discussion groups at this Congress.

What are the reasons for this renewed activity? There is first of all the realization how sadly the classification of birds had been neglected during the era of the new systematics and in what deplorably bad condition it was. This new interest led to the search for, and the discovery of, whole sets of new characters which made the task of finding an improved classification far more hopeful. Equally important was the fact that a new interest in the concepts of classification developed in the period after 1950 and that the heated controversies on some of the new theories helped to revive an interest in macrotaxonomic research. Both preconditions were obviously highly necessary because in order to establish a sound classification one must first have a sufficient number of characters to work with, and one must secondly have a sound conceptual framework within which to develop one's conclusions.

Taxonomic characters

Let us begin with the problem of taxonomic characters. In the early stages of taxonomy, for instance in ornithology in the 18th and early 19th centuries, classifications served simultaneously also as identification keys. This necessitated the basing of classifications on single characters: feet with webs or not; bill hooked or not. Perceptive authors, from the very beginning, recognized that the tyranny of single characters leads to the establishment of artificial groups based on convergence. John Ray, as well as Buffon and his followers, proposed instead, in contrast to the Linnaeans, to base classifications on an ensemble of characters.

As much as ornithologists pay lip service to the fallibility of single characters, nevertheless whenever a new taxonomically useful character is found, it tends to be made the basis of rather sweeping taxonomic proposals. This has been true for the structure of the syrinx, certain muscle patterns, the scutellation of the tarsus, the number of notches on the sternum, or the form of the stapes. All of these characters have given us valuable information but I rather suspect that not a single one of them is infallible and that all of them occasionally break down.

The foundation of all of our classifications is still given by morphological characters. Since Bock (1975) has reviewed at Canberra the contributions to avian taxonomy made by morphologists, I shall not cover the same ground again. He gave a characterization of what are "good taxonomic characters" and has emphasized correctly that different characters must be used at different levels of the taxonomic hierarchy. Morphological characters are particularly valuable because some of them permit a connection with the fossil record. Yet, much of the morphological analysis concerns characters that do not fossilize, like the syrinx, the various muscle systems, the intestinal tract, and the sense organs. Exactly in this area some excellent studies have been made in recent years, such as those of Ziswiller on the intestinal tract, and some unexpected discoveries have been made. Olson (1973) has shown us how much the classification of a family of birds can be improved simply by an intelligent evaluation of morphological characters, the rails being the group he studied.

The Boat-billed Heron *(Cochlearius)* is a typical case where a conspicuous morphological specialization has not yet been fully elucidated. Wetmore (1930), owing to its peculiar bill, considered this bird the representative of a separate family, while Heinroth and following him Bock (1958), thought that this heron, except for its broad bill, was a typical night heron and should not be given more than generic rank; Payne & Risley (1976) removed the bird again from the night herons and gave it the rank of a tribe. It was generally assumed that the broad bill had developed as a special feeding adaptation but the latest reports seem to indicate that the feeding habits of the boat-bill are identical with those of the night herons. What then is the meaning of this unusual bill? Is it a courtship adaptation (connected with bill clapping) and if so how highly should it be regarded? I am using this case simply to illustrate the kinds of difficulties one encounters in the evaluation of morphological characters. I shall presently say more about the use of characters in classification, but want first to say a word about the fossil record.

Classification and the fossil record

Nearly 20 years ago I made the claim: "I think, it is fair to state that with the spectacular exception of *Archaeopteryx,* there is not a single case in which a fossil bird has helped us

to improve our classification" (1959:296). One may argue whether this statement was valid even in 1959 but, considering the richness of new fossil material described since that date, one can certainly argue whether it is still true.

In order not to be misunderstood, let me emphasize that we are dealing with two very different kinds of problems, (1) a better understanding of previously known taxa or phyletic lines, and (2) the discovery of new fossils which represent "missing" links between phyletic lines not previously known to be related. As far as (1) is concerned, research on fossil birds has indeed made great progress in recent decades. A renewed study of fossil material has revealed numerous cases where certain genera or even families had been misidentified or been placed in the wrong higher taxon. Many species and genera described by the pioneers of paleornithology had to be synonymized or shifted to different families or orders. Previously claimed relationships were refuted. Typical examples are the Australian family of Dromornithidae which PAT RICH showed to have nothing to do with the New Zealand Moas or the revising of the fossil Gruiformes and moas by CRACRAFT. The more careful morphological analysis of the younger generation of students has led to a far better understanding of fossil birds. The new discoveries concerning *Archaeopteryx* and the Cretaceous toothed birds is splendid evidence.

Archaeopteryx

That the birds are derived from the reptiles and that the Jurassic fossil *Archaeopteryx* is an almost ideal missing link, has been uncontroversial for generations. It was likewise understood that the birds originated from that branch of the reptiles called the Archosauria, to which also belonged the pterodactyls, crocodilians and dinosaurs. What was controversial, however, was the exact place within the Archosauria that had given rise to the birds. HEILMAN, in his well-known monograph on *Archaeopteryx*, opted for an early origin, that is from a group called the pseudosuchians, thus before the actual split of the archosaurians into the various branches. If this interpretation were correct, the birds would be first cousins to the dinosaurs and crocodilians. This view has been challenged in a recent reanalysis by J. H. OSTROM, who made a very string case in favor of a direct derivation of the birds from a group of coelurosaurian dinosaurs. To be sure, this conclusion must be tested, but if it should be correct, it raises some interesting questions. For instance, I do not agree with the assertion of some cladists that the new analysis forces us to rank the birds among the dinosaurs, as a suborder of winged dinosaurs. As far as I am concerned the invasion of the new adaptive zone by the ancestors of the birds has resulted in such a drastic reorganization of morphology, physiology, and behavior that it would be just as misleading to call birds winged dinosaurs as it would be to call the mammals hairy reptiles.

Although basically this has nothing to do with the classification of the birds, the new theory of the origin of the birds has once more raised the problem of the origin of flight. There is little doubt that the early proaves had feathers before they had wings and before they were able to fly. Among the various theories of the origin of feathers that of REGAL (1975) is most persuasive who considers them an adaptation, originally against overheating and eventually as facilitating, quite generally, temperature regulation during an early period of not yet fully developed endothermy.

The coelurosaurians, from which Ostrom derives the birds, were small terrestrial, more or less bipedal, reptiles. The classical theory of the origin of bird flight is that the ancestors of *Archaeopteryx* were arboreal, jumping from branch to branch, used the feathers on their anterior extremities to prolong their jumps, eventually were able to glide and finally shifted to active beating of the wings. Ostrom considers this unlikely since he does not believe that a terrestrial running coelurosaurian has the type of legs and feet that are suitable to jump on to branches of trees and from branch to branch. He favors a theory, first promoted by Nopcsa (1907), that the proaves were running ever faster until they had sufficient speed to be lifted off the ground by the spreading of their forearms. The Nopcsa theory never had much support among paleobiologists because upright, bidepal walking and running in reptiles led in all other cases to a reduction of the anterior extremities. To cope with the difficulty Ostrom proposes that birds had a second function for their winged forearms, that of catching and holding prey. To me, this seems an improbable theory, for such a function of the forearms would require great strength and heavy musculature which is conspicuously lacking in *Archaeopteryx*. For this reason I still favor the arboreal theory of the origin of bird flight. Furthermore, it would seem by no means very difficult for running bipedal birds to jump onto branches and to perch on trees. The transition toward gliding is certainly far easier for an arboreal proavis than for a running one. What is needed now is a more detailed analysis of the foot of *Archaeopteryx* and of the coelurosaurian dinosaurs to determine to what extent they could have been arboreal, and of the wing of *Archaeopteryx* to determine whether or not it could have had a function other than gliding before it became a bird wing.

The Cretaceous toothed-birds

The reptilian origin of birds was further cemented by the discovery of two kinds of extinct Cretaceous toothed-birds, *Hesperornis* and *Ichthyornis*. Until recently there has been considerable uncertainty about these fossils, indeed it was even questioned whether the pieces of toothed jaws found with the avian skeletons really belonged to these birds, or rather to reptilian species associated with them in the same deposits. We are now fortunate to have a modern analysis of these remarkable early birds which sheds a good deal of new light on avian phylogeny. Gingerich (1977) has not only clearly demonstrated that both types indeed had teeth in their jaws but he has also discovered that *Hesperornis* has a palate that has all the characteristics ascribed to the palaeognathous palate of the ratites but which is also found in the theropod dinosaurs that gave rise to birds. This poses a number of entirely new questions. *Hesperornis* is a highly specialized type of bird but the general conformation of *Ichthyornis* is not too different from that of a modern bird (it has been compared with a gull) except for the teeth. It would seem safe to postulate that all primitive birds were palaeognathous. This type of palate can therefore no longer be considered a synapomorphy of the various types of ratites and of the tinamous, as was done in the recent literature.

Let us attempt to summarize the contributions of paleornithology to avian classification. Fossil birds have taught us a great deal about relationships within the avian orders, about the relationship of families, and about the rate of change from the late Cretaceous and early Tertiary to the present. But when it comes to the discovery of true missing links between orders of birds, my statement of 1959 is, I believe, still true. No intermediates have been

found, up to now, between, let us say penguins and Procellariiformes, or between parrots and pigeons, or between woodpeckers and songbirds, or between any other of the higher taxa of birds that are suspected of being related. I am saying this in full awareness of the claims made for *Presbyornis*.

This is particularly disappointing considering the rapidity with which the fossil record is expanding. Yet, no matter how far back one goes, the fossil pelicans still are pelicans, and the fossil penguins are still much like modern penguins. The few cases where it was claimed for certain fossils that they represent such missing links are either controversial or have since been refuted.

The greatest contribution which the fossil record has made is to paleozoogeography. For instance, when we want to determine what higher taxa of birds belong to the southern Gondwana element and which others to the northern element, fossils have often made a decisive contribution, as in the case of the Cracidae and Cathartidae.

The continuing absence of missing links in spite of the wealth of new discoveries makes me suspect that we will find in birds the same situation as in almost all groups of fossil animals: the origin of a new taxon seems to be such a rapid event that the probability of the preservation of the intermediate steps in the fossil record is utterly improbable. The scarcity of missing links between major avian taxa therefore, is something not altogeher unexpected.

Before concluding my remarks on morphological characters, let me emphasize how great a contribution to avian classification I still expect from morphology. There are numerous aspects of avian morphology that have not yet been investigated at all, and the analysis of the characters that have been used in the past, could be considerably expanded in breadth and depth.

Non-morphological characters

Disappointed by the seeming failure of morphological characters and of the fossil evidence to give us definitive answers in our search for the relationship of the major taxa of birds, some ornithologists in recent years have increasingly turned to a search for new kinds of characters. The large repertory of behavioral characters seemed at first sight, to be able to provide a most useful set of such characters. This included vocalizations, courtship displays, predator thwarting activities, comfort movements, activities connected with nest building and the raising of young and many others. This expectation was not altogether disappointed and after the pioneering efforts of WHITMAN and HEINROTH numerous ornithologists employed behavioral characters in their endeavors to improve classification. I have summarized much of this endeavor at an earlier occasion (MAYR, 1958). Eventually, it turned out, unfortunately, that behavioral characters are the less useful, the higher up we go in the taxonomic hierarchy. They are most useful at the level of the species and the genus, less so at the level of the family, and virtually useless at the ordinal level, precisely where we are in the greatest need of finding additional characters. There are a few exceptions, like the behavioral similarities between Galliformes and Anseriformes, but otherwise this generalization is valid. Behavioral characters are particulary subject to multiple, convergent origins, as demonstrated by "scratching over or under the wing" or the mode of drinking.

The convergence in behavioral characteristics, correlated with habitat or food niche, deserves far more attention than it has so far received. The hawking behavior of a true flycatcher, let us say *Muscicapa striata,* is extraordinarily similar to that of certain tyrant flycatchers, let us say, the phoebe *(Sayornis).* The Australian flycatchers *(Microeca* group) are, as Sibley has shown, a third convergent development. To give another example, we find in virtually every continent a genus of birds, resembling the European wagtail *(Motacilla),* and adapted to life on torrents or brooks. Even though these genera are quite unrelated they all have similar behavior specializations. Let me mention one other case of behavior convergence which led me to wrong conclusions. It concerns the Australian scrub robin, *Drymodes,* which some authors have placed with the thrushes, others with the babblers. When I was able to observe the bird in Australia in 1959, I discovered that it seemed to agree with thrushes like *Hylocichla,* in its hopping, wing and tail movements, grasping of food, etc. Clearly, I said, *Drymodes* must be a thrush and not a babbler. Now Sibley's DNA matching has revealed that *Drymodes* is neither a thrush nor a babbler, but the derivative of an autochthonous Australian song bird assemblage. And this poses the interesting question: What is the selective advantage of having movements like a thrush if one is a ground feeder like a thrush? Furthermore, it once more opens up the whole problem of the taxonomic information content of behavioral adaptations. Meise (1963) has shown very convincingly in how many behavioral characteristics the various orders of ratites resemble each other, but there is still the remote possibility that some of these similarities are adaptive, acquired secondarily after the loss of flight and after the acquisition of a terrestrial, running mode of life.

As with all characters, one must exercise great caution with behavioral characters. Even in the comparison of vocalization, there is always the possibility that certain sibling species do not differ noticeably in their songs. There is a group of sibling species of honey eaters in New Guinea, the *Meliphaga analoga* group, in which several field workers up to now have been unable to find differences in vocalization. Frankly, I would be greatly surprised if differences were not eventually found, but it is evident that they cannot be very conspicuous.

More dangerous for the taxonomist is another problem. Owing to the fact that good sympatric species nearly always differ in their songs, the conclusion is sometimes wrongly made that geographic isolates must be raised to species rank if they differ in their songs. However, this is not true. We now know that in many species song varies geographically in a rather drastic manner. Since the deviating populations are connected, in most cases, by intermediates we know that they are conspecific. Hence, it is not admissible to treat an allopatric polulation as a different species merely because it has a different song.

Macromolecules as taxonomic characters

A major new complex of taxonomic characters has been discovered in the last 25 years, the macromolecules. Only the specialist can appreciate the extraordinary complexity of the proteins, nucleic acids and other macromolecules, as well as the enormous amount of information they contain. One approach to the study of proteins, serological comparisons, is actually more than 75 years old, but, as applied to avian taxonomy, it was very inaccurate and produced no useful results. The first ornithologist who applied the methods of macromolecular analysis consistently for systematic purposes was Charles Sibley.

With great determination he employed one method after the other and even though, as he would be the first to admit, some of his earlier methods were not reliable, he discovered the misclassification of a number of avian genera, as for instance *Zeledonia*. I shall not attempt to point out the strengths and weaknesses of the various methods beyond saying that the method of electrophoresis is more useful for the comparison of populations and closely related species than for the purposes of macrotaxonomy. The method of amino acid sequencing has produced some extremely interesting results but is very costly in terms of time and equipment and cannot be done routinely.

For a number of reasons various methods of DNA analysis are actually to be preferred, and Drs. SIBLEY and AHLQUIST have shown at this Congress what exciting results they were able to obtain with the relatively simple technique of DNA hybridizing. Methods of DNA sequencing are now also being developed in various laboratories and I am told that these methods are less complicated and more reliable than amino-acid sequencing. I have no doubt whatsoever that we are at the threshold of spectacular advances. I share Dr. SIBLEY's conviction that these molecular methods, together with the morphological evidence, will give us in due time what STRESEMANN had considered as impossible, that is, clear-cut evidence as to the relationship of the higher taxa of birds.

Some of the results produced by the new methods were quite unexpected. The American Turkey, for instance, which looks so strikingly different from any kind of gallinaceous bird found in the Old World turns out, on the basis of several independent tests, to go right in with the pheasants, and to be actually more similar to *Phasianus* than is the chicken.

Where the new methods are particulary useful is in revealing cases of convergence. It had of course long been known that the tyrant flycatchers and American woodwarblers are not at all related to their Old World counterparts, the true flycatchers (Muscicapidae) and the true warblers (Sylviidae). What we did not appreciate until this was revealed through Dr. SIBLEY's researches was that the Australian flycatchers (Monarchinae) and robins (*Eopsaltria* and relatives) as well as the Australian warblers (Acanthizinae and Malurinae) and the shrike-like whistlers (Pachycephalinae) have nothing to do with their north-temperate counterparts but are an autochthonous adaptive radiation in Australia, all these types being more closely related to each other than to their Eurasian-African counterparts. Since these Australian flycatchers and warblers are species-rich groups, the new assignment has a major impact on the classification of the song birds (Oscines).

How to use taxonomic characters?, or taxonomic philosophies

Prior to DARWIN, and unfortunately very often also after DARWIN, classifications were based simply on degrees of similarity. The most similar species were grouped into genera, the most similar genera into families, and so forth up the taxonomic hierarchy. However, as soon as DARWIN's theory of evolution by common descent was accepted, it became clear that taxa had to consist of descendants from a common ancestor, they had to express relationship. But how to accomplish this has been the source of much controversy, particularly in recent decades. DARWIN stated quite specifically how a classification should be constructed. It should be based on two considerations: Each taxon should be monophyletic, that is it should include only descendants of a common ancestor, but the ranking of these taxa should be based on the degreee of their evolutionary divergence. For instance, even though bird and dinosaurs have a nearer common ancestor than dinosaurs

and turtles, nevertheless the evolutionary divergence of birds is so great that they deserve to be ranked as a class, corresponding to all reptiles. Darwin's recommendations have formed the traditional basis of biological classification ever since 1859. However, the evaluation of degree of evolutionary divergence is unavoidably based on an exercise of judgment and was therefore attacked in recent decades as arbitrary and subjective. Two new taxonomic philosphies were proposed instead, both with the claim that they were objective and would lead to the adoption of a universally accepted classification.

One of the two recently proposed taxonomic philosophies is phenetics, primarily promoted by Sokal, a non-taxonomist by background. It aims to avoid any subjectiveness of classification by basing taxa on large numbers of characters, all of them given equal weight. The experience of the last 25 years has shown that this method is reasonably successful when applied to previously chaotic groups or to genera with very large numbers of species but that it has been unable to make any contributions to the classification of mammals, birds, or any other group with a reasonably mature classification.

The other of these schools, cladistics, places its entire emphasis on genealogy, the splitting of the phyletic lines. Each such split, say the cladists, creates two sister groups which have to be given the same taxonomic rank. The strength of the cladistic method is that it insists on a rigorous determination of the monophyly of every taxon. I agree with the cladists that this is the only way by which to achieve relatively homogeneous taxonomic groups, and that one must have such homogeneous groups in order to be able to make universally valid statements and on which comparisons with other taxa can be safely be used.

The cladistic method, however, has two great weaknesses. The first is that it bases the delimitation of taxa exclusively on synapomorphy, that is on the possession of characters derived from a common ancestor and not found in the sister group. The determination of synapomorphy, however, encounters three serious difficulties, which are underestimated, if not entirely ignored, by most cladists. I do not have the time to discuss these difficulties in detail, but let me at least mention them.

(1) The difficulty of determining the relative primitiveness of a character, or what in German is called die Leserichtung of a series of characters,

(2) Convergence, which requires making the decision whether the morphological similarities of two groups, let us say grebes and loons, is due to common descent or due to convergent adaptation, and,

(3) Mosaic evolution, that is unequal rates of evolution of different characters.

Each of these three difficulties requires a certain amount of subjective evaluation, and makes cladistic analysis far less objective than is generally claimed.

Even more serious is another weakness of cladistics, which is that the method ignores entirely the second one of Darwin's criteria, the degree of evolutionary divergence. It would force the cladists, for instance, to give to the coelurosaurian dinosaurs the same categorical rank as to the entire class of birds. Inevitably a strict application of the cladistic method leads to rather unbalanced classifications.

One reason why both cladistic and phenetics have proven unsuccessful is that in the last analysis both methods base all their conclusions on a single criterion, cladistics on branching points, and phenetics on a calculated measure of overall unweighted similarity.

Evolution is a highly complex process, and groups of organisms, the product of evolution, can be correctly delimited and ranked only if all processes of evolution are considered and carefully evaluated. In spite of their weaknesses, both of these two new philosophies, cladistics and phenetics, have given us new insights and have been responsible, to a considerable extent for the great recent interest in classification and macrotaxonomy.

The most important insight gained as a consequence of these developments is that characters do not automatically produce a classification.

The many convergent characters discovered by the morphologists were the first indication of this difficulty. Let me remind you only of the hooked bill in hawks, owls, and shrikes, or the webbed toes of many water birds, or the tubular tongue of nectar feeders. I am afraid we may have to transfer the lesson we have learned from morphological characters also to the molecular characters, or at least to some of them.

The fact that Man und chimpanzee have many identical macromolecules does not necessitate placing both in the same genus. Here we have also an excellent illustration of mosaic evolution, because other components of the genotype of these primates have drastically diverged since the two lineages separated in the Miocene.

Let me reenforce this consideration by a case taken from ornithology. JOLLÈS & WILSON (1976) showed through a sequence analysis of the amino acids of avian lysozymes that the Cradidae differ from the Old World gallinaceous birds (pheasants, etc.) by numerous amino acids, so that one must conclude that they separated a long time ago. When these authors studied the lysozymes of the waterfowl JOLLÈS and WILSON found, that the Anseriformes share more amino acids with the Old World gallinaceous birds, than the latter with the Cracidae.

The almost inevitable conclusion one must derive from this situation is that the Anseriformes branched off from the Old World gallinaceous birds either later but certainly not earlier than the Cracidae. Two independent immunological methods have confirmed the close relationship of waterfowl and gallinaceous birds. On the other hand according to SIBLEY's DNA findings the Anseriformes are not particularly closely related to the gallinaceous birds, and according to classical morphology Cracidae and Old World gallinaceous birds are far more closely related to each other than either is to the Anseriformes.

What should the avian taxonomist do in the face of these conflicting interpretations? Should he make a separate order for the Cracidae and combine pheasants and Anseriformes in a single order, as cladistic theory might demand?

I hope not! A proper Darwinian emphasis on the importance of evolutionary divergence will still permit us to maintain the Anseriformes as a separate order, and to keep the Galliformes as a single order. The only change we have to make in our avian classification, if the JOLLÈS-WILSON interpretation is correct, is to place the Anseriformes next to the Galliformes, and preferably after them, since they seem to be derived from them.

Ever since a science of taxonomy has existed, ornithologists have been searching for the ideal classification. When the morphological and behavioral characters failed, it was hoped that chemical or molecular criteria would bring salvation. Indeed, serology, immunology, egg white proteins, and blood proteins, they all yielded some information, but none of them provided the hoped for panacea.

Will the nucleic acids be able to be successful where all other molecules have failed? They certainly give cause for hope, because they reflect the total genotype far more completely than any of the other molecules used in chemical taxonomy. Yet, caution is still advisable, since we have been disappointed too often in the past. And there is a special reason why we should be cautious. The researches of recent years have revealed that the DNA of a species is a highly heterogeneous composite.

Even the unique DNA seems to consist of many different types; enzyme genes, regulatory genes, immune genes, and possibly other as yet unknown kinds. The indications are (A. C. Wilson) that enzyme genes and genes controlling morphological changes have different evolutionary rates, and it is rather probable that evolutionary rates of the different nucleic acids are different from each other and different in various kinds of organisms. The more nucleic acids are subject to mosaic evolution the less useful they will be as indicators of relationship. At what distance of relationship DNA matching will lose its value is still quite uncertain. In spite of this appeal to caution, I share the optimism of those who, like Sibley, think that DNA analysis, together with some of the methods of protein analysis and the more traditional methods of morphology, will eventually provide a great deal of decisive information on the relationship of the higher taxa of birds.

Let us tentatively assume, that newly discovered characters will eventually give us all the information needed to determine the nearest relatives of each higher taxon of birds. But thus will not be the end of our quest, for determining the relationship of individual taxa is only the first step in making a classification. One also has to determine in what sequence one wants to list these taxa, since they are arranged in a linear sequence in faunas, books, and museum collections. And to arrive at the best possible linear sequence is difficult at best.

In the days when one still believed that evolution was a progression from lower to higher, one thought that the method of classification was quite simple. One started the linear sequence with the most primitive taxon, and moved up to the highest, to the most advanced one. But the facts to not confirm this ideal. Among birds there was apparently a very early radiation leading to the development of a multi-branched phylogenetic bush, with many, more or less equivalent, branches. The same broad radiation seems to be true for the families of songbirds as confirmed by Professor Sibley's researches.

Each of these branches may specialize in an evolutionary elaboration of some special structure or organ system, be it the wing, or the central nervous system, and there are not independent criteria that would tell us, which ones of these specialized groups should be considered higher, and which other ones lower.

But this absence of linearity in avian evolution is not the only obstacle in our path towards the perfect classification. We also have to find a solution for the problem of highly unequal rates of divergence, (a) of different structures and organ systems (mosaic evolution), and (b) of the different branches of the tree. The case of the relationship of gallinaceous birds and Anseriformes illustrates the kind of difficulties I have in mind, and so does the relationship of man and chimpanzee.

Could these difficulties perhaps be overcome by making use of the so-called "molecular clock," to determine the relative age of the various avian taxa? If rate of evolutionary change at the molecular level were uniform, one could – and this has actually been

proposed by A. C. WILSON – list all taxa according to the degree of molecular difference from a common ancestor. With the crocodiles being the nearest living relatives of the extinct proavis, one could use them as evolutionary base line and list all avian taxa according to their degree of difference from the crocodiles. However, it is doubtful that this ingenious solution would work, since there are more advanced and less advanced genera and families on each of the branches of the avian bush.

For all these reasons, I am afraid, there is no simple solution for the problem of finding the perfect classification of birds. No instructions exist that would tell us how to convert a phylogenetic bush into a linear sequence of the higher taxa of birds. I believe that the only way this problem can ever be solved is by international agreement. And that is the current status of the problem of avian classification.

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Biological Clocks in Birds

Jürgen Aschoff

Introduction

Organisms are adapted not only to the mean prevailing conditions of their environment but also to variations of conditions around these means. To simplify matters, one can make a distinction between two types of variations. First, there are variations that are unpredictable because they occur more or less at random. One evolutionary strategy to cope with variations has been the development of homeostasis that renders organisms partly independent of changes in environmental conditions. Other environmental variations are characterized by predictability because they occur periodically. Most important examples of these are daily and seasonal periodicities. To cope with these temporal programs in the environment, an obvious strategy is to incorporate into the genetic make-up of the organism similar programs, i.e. to equip the organism with biological clocks which enable the individual to adjust its activities in advance to ensuing changes in environmental conditions.

In this article evidence will be presented supporting the idea that there occur in birds two kinds of such clocks: circadian clocks adjusted to the rotation of the earth around its axis, and circannual clocks adjusted to the rotation of the earth around the sun. The discussion concentrates on a few important features of these two classes of clocks, with a deliberate (over-) emphasis of similarities between them. In speaking of clocks, we do not refer to hourglass mechanisms which might be adequate time-telling devices for some organisms and for special purposes. Instead we will restrict ourselves to 'true clocks' in the terminology of the physicist, i.e. to periodic processes in the special sense of selfsustaining oscillations.

Properties of circadian clocks

Freerunning circadian rhythms and their entrainment by zeitgebers

An overt rhythm is likely to be based on a selfsustaining oscillation, if a) the rhythm continues in constant conditions without damping, and b) the frequency of the then 'freerunning' rhythm deviates from that of the corresponding environmental periodicity. Examples of such freerunning rhythms are provided in Fig. 1 which shows oxygen consumption in two Chaffinches (*Fringilla coelebs)*, first kept in light-dark cycles of 12 : 12 hours (LD), thereafter in conditions of constant dim illumination (LL). In both records, the rhythm of oxygen uptake continues in LL without damping, and the period τ deviates from 24 h by +0.8 h (above) and -0.9 h (below), respectively. As a consequence, there is a steady drift of the phases of the rhythms, e.g. of the maximal values, against time of day: on consecutive days, the maxima occur progressively later in the upper record, and progressively earlier in the lower record. The conclusion seems justified that both records

This paper is dedicated to Prof. Dr.-Dr. hc. Konrad Lorenz on the occasion of his 75th birthday.

Co-authors: Peter Berthold, Eberhard Gwinner, Hermann Pohl and Ursula von Saint Paul.

Author's address: Max-Planck-Institut für Verhaltensphysiologie, 8131 Andechs, Bundesrepublik Deutschland.

represent, in LL, truly freerunning 'circadian' rhythms (ASCHOFF 1960), reflecting the behaviour of selfsustaining oscillators (PITTENDRIGH 1960). During the first 6 days of the experiment, these oscillators are synchronized to the light-dark cycles that act as entraining forces or zeitgebers (ASCHOFF 1951).

As can further be seen from Fig. 1, the wave forms of the rhythms are different in the two conditions: whereas 'plateaus' are indicated in L as well as in D during entrainment, the curves become more sinusoidal in LL. This illustrates the often described two-fold effects of a zeitgeber which not only entrains the circadian oscillator (the 'clock') via control of its phase but also influences the overt rhythm at a more peripheral level; as a consequence, entrained rhythms often differ in shape and amplitude from freerunning rhythms (cf. rhythms of brain temperature in chickens; ASCHOFF & SAINT PAUL, 1972). The physiological mechanisms of such 'masking effects' (ASCHOFF 1960) are still obscure; they are mentioned here because of the possibility of similar effects in the interaction between circannual rhythms and their zeitgebers (cf. Fig. 15).

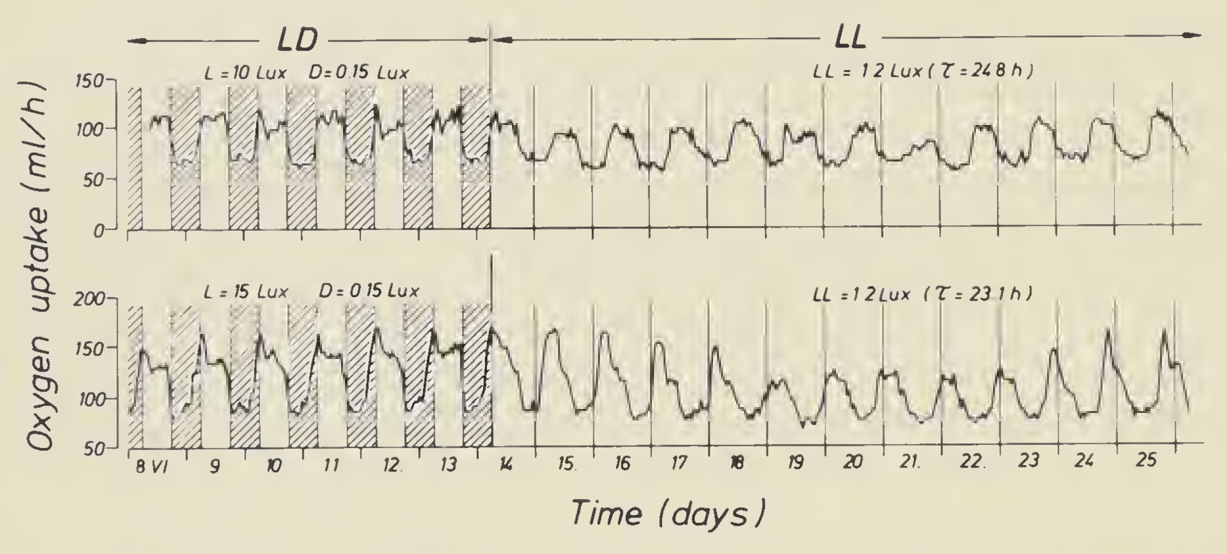


FIGURE 1. Circadian rhythms in oxygen uptake in two Chaffinches, *Fringilla coelebs*, kept for 6 days in light-dark cycles (LD), thereafter in constant dim illumination (LL). τ: mean circadian period.

Finally, Fig. 1 illustrates the inter-individual variability of τ-values measured in LL, and its bearing on phase-control during entrainment. During entrainment, oxygen uptake starts to rise before the transition from D to L. The interval between increase of oxygen uptake and light-on, the phase-angle difference (ψ), is larger in the lower record than in the upper record; on the other hand, τ measured in LL is longer in the upper than in the lower record. This apparent dependence of the phase-relationship between the entrained rhythm and its zeitgeber on the period of the freerunning rhythm reflects a genereal rule which is illustrated in diagram A of Fig. 2. Two oscillations are drawn that freerun in constant conditions with a high and a low frequency, respectively. After they have become entrained by a zeitgeber of medium frequency, the fast oscillation phase leads the zeitgeber – its phase-angle difference ψ is positive – and the slow oscillation phase lags the zeitgeber – its phase-angle difference ψ is negative (ASCHOFF 1965).

The rule just explained also applies when an oscillation of medium frequency becomes entrained by a zeitgeber of either higher or lower frequency. As shown in diagram B of Fig. 2, entrainment by the 'fast' zeitgeber (with a relative short period) results in a

phase-lag (negative ψ), and entrainment to the 'slow' results in a phase-lead (positive ψ). To study the systematic changes of ψ as a result of changes in zeitgeber period has become a useful tool in analyzing features of oscillating systems. Examples are discussed in the following section.

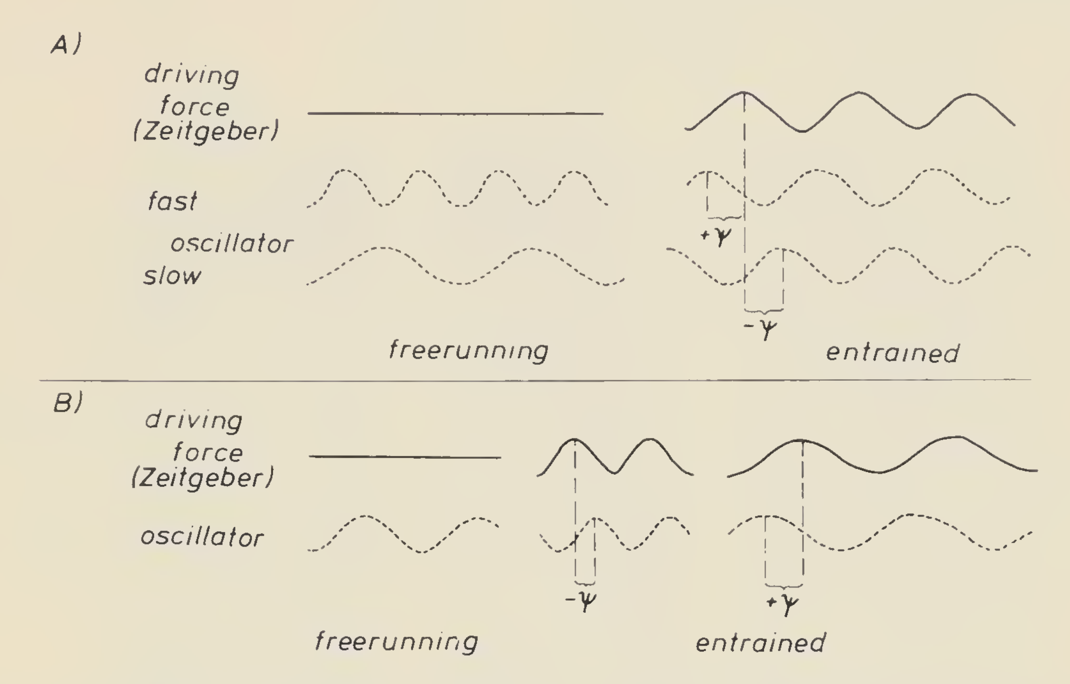


Figure 2. Schematic illustration of principles of entrainment.
A) Left: two oscillations (dashed curves) freerun in constant conditions with different frequencies. Right: when entrained to the same zeitgeber of medium frequency (solid curve), the fast oscillation phase leads, and the slow one phase lags the zeitgeber.
B) An oscillation of medium frequency (left), when entrained phase lags a zeitgeber of higher frequency (middle), and phase leads one of lower frequency (right). ψ: phase-angle difference between entrained oscillation and zeitgeber.

Range of entrainment and change of phase-angle difference

The range of periods within which entrainment can be achieved is limited. Its width depends of the 'strength' of the zeitgeber for a particular organism. 'Strength' as used here comprises the physical characteristics of the zeitgeber, especially its 'amplitude' (e.g. the difference in intensity of illumination between L and D), as well as the sensitivity of the organism to the stimuli of the zeitgeber (Aschoff, 1960). The stronger the zeitgeber, the larger a range of entrainment, and the smaller variations in ψ, can be expected. To illustrate this, original records of locomotor activity of threee Canaries (*Serinus canaria*) are reproduced in Fig. 3. For the first ten days, the birds have been kept in conditions of constant dim illumination, thereafter in LD-cycles with 50% L in each cycle for days 11 to 31, followed by cycles with 25% L. The middle record shows entrainment to a zeitgeber period T of 24 hours, the left one to 22 h, and the right one to 26 hours. In constant conditions prior to entrainment, all three birds exhibit freerunning rhythms with periods close to or slightly shorter than 24 h. During entrainment to the zeitgebers with 50% L and 50% D, the three records differ with regard to the phase-relationship between rhythm and zeitgeber. In accordance with the rule illustrated in diagram B of Fig. 2, the phase-angle difference between onset of activity and light-on (ψ_{onset}) is close to zero in T = 22, slightly positive in T = 24 h, and more positive in T = 26 h. After the shortening of L to

25% (without a change in period), the differences in ψ-values become larger due to further advances of onsets in the middle and the right record. In the left record, there is no change in ψ_{onset} but activity stretches into D by several hours. The increase in phase-angle difference between rhythm and zeitgeber after the reduction of L from 50% to 25% (in the middle and right record) indicates that a LD-cycle with 25% L provides a less strong zeitgeber than a cycle with 50% L.

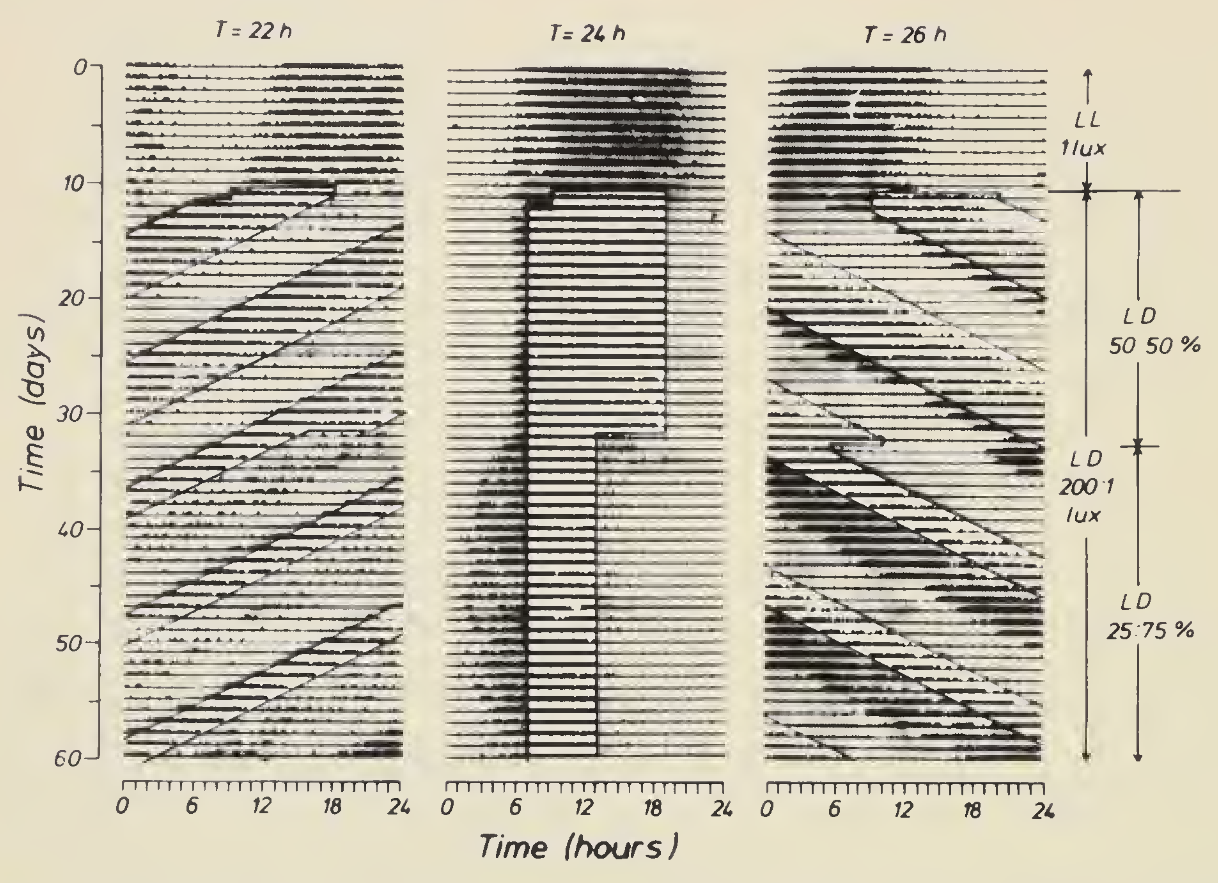


FIGURE 3. Original records of locomotor activity of three Canaries, *Serinus canaria,* kept for ten days in constant dim illumination (LL), thereafter in light-dark cycles (LD) with 50% L, followed by cycles with 25% L. T: period of the LD-zeitgeber. Shaded area: 1 lux. White area: 200 lux. Activity indicated by black marks or bars.

Apart from effects on phase, entrainment of an activity rhythm by zeitgebers of various periods and of different L : D-ratios influences the amount of activity and its pattern. This is demonstrated in Fig. 4 the diagrams of which represent the mean pattern of activity of 9 Canaries averaged over 10 cycles for each individual. For both types of zeitgebers, middle of dark-time is used as a reference phase (= zero at the abscissa). Comparison of the three rows of Fig. 4 indicates that the amount of activity decreases from T = 26 h to T = 22 h. Comparison of the two columns shows on the other hand, that the 'amplitude' of the activity rhythm is generally larger during entrainment to a zeitgeber with 50% L as compared to a zeitgeber with only 25%. Entrainment to the latter type of zeitgeber further illustrates especially well 'masking effects', i.e. the depression of activity in D after its "too early" onset, and its "re-boosting" when the lights are turned on (cf. the records in T = 26 h and T = 24 h). Finally, the changes in phase-angle difference due to changes in T are indicated by connecting a) onsets of activity (dashed lines) and b) midpoints of activity-time (bold closed circles). The difference in slope between these lines – larger inclination for L = 25% than for L = 50% reflects the difference in strength between the two types of zeitgebers.

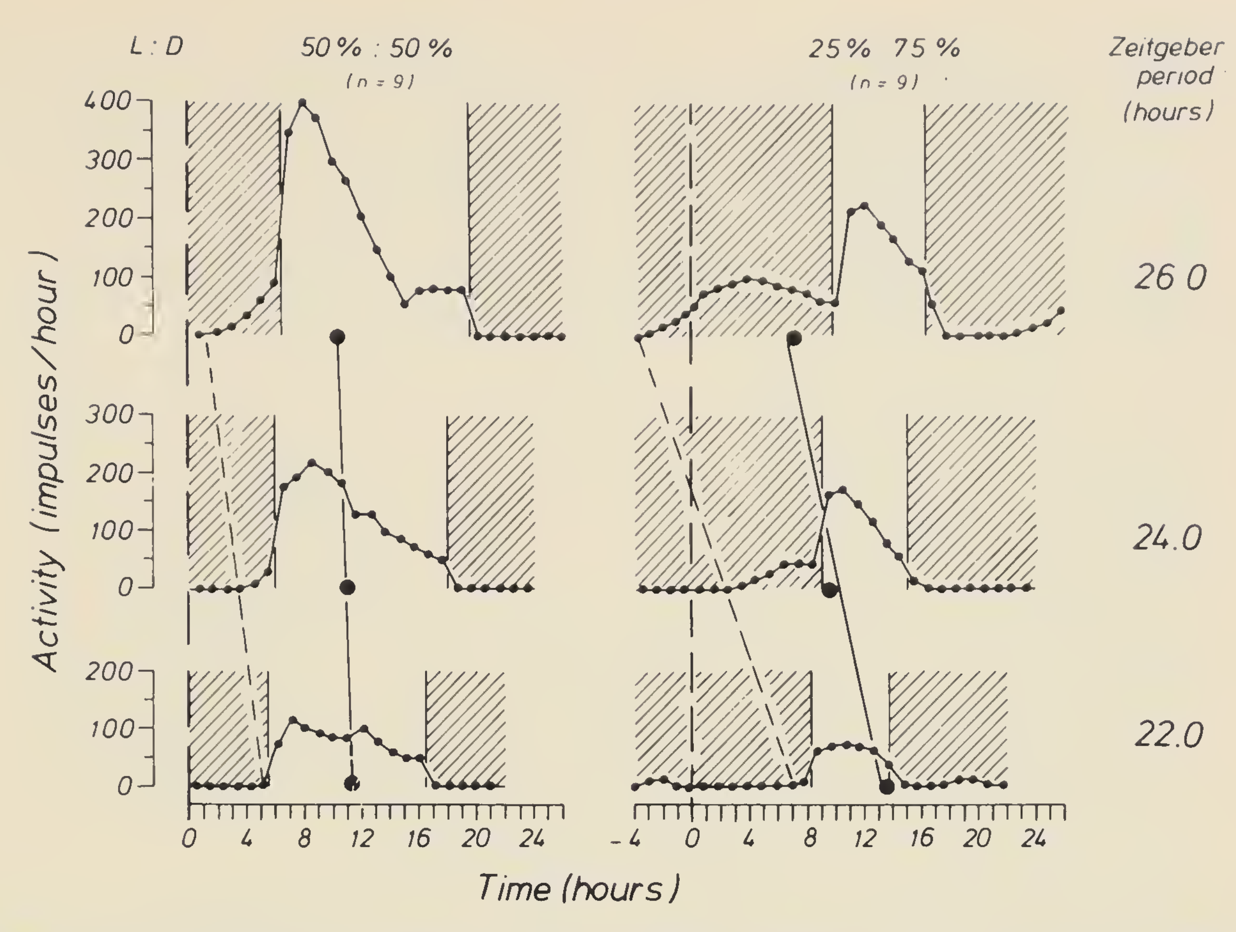


FIGURE 4. Hourly values of locomotor activity of caged Canaries, *Serinus canaria*, kept in light-dark cycles (LD) of three different periods (right margin) with either 50% L (left) or 25% L (right). Mean pattern from 10 cycles each. Onsets of activity connected by dashed lines, midpoints of activity time (bold closed circles) by solid lines.

The dependence of phase-angle difference on zeitgeber period has been tested in a variety of avian species. Most of the results are summarized in Fig. 5 (The way in which the two diagrams are drawn can be understood if the system of coordinates used for Fig. 4 is rotated clockwise by 90°). The abscissa represents zeitgeber period, and the ordinate time before or after a reference phase of the zeitgeber. However, time is now expressed in degrees, instead of in hours, with each zeitgeber period corresponding to 360°. Hence the ordinate represents the phase-angle difference ψ between a phase of the circadian rhythm – usually onset of activity or middle activity-time – and middle of dark-time of the zeitgeber (= zero degree). In both diagrams the "phase curves" which describe changes in as a function of changing zeitgeber period, obey the rule that an increase in zeitgeber period is correlated with an increase in ψ (decrease of negative values or even change into positive values). It is also obvious that, in the left diagram, the curves encompass a smaller range of periods than in the right diagram, and that their slopes are steeper. This is because data from experiments with relatively weak zeitgebers are summarized in the left diagram, and data from eyperiments with relatively strong zeitgebers in the right diagram (cf. the figures for light intensities given in parentheses after the species names). Hence, small ranges of entrainment are to be seen in the left, and larger ranges in the right diagram. According to a recent analysis (Aschoff & Pohl, 1978), circadian rhythms change their phase-angle difference to the zeitgeber within the complete range of entrainment by a similar amount of degrees, irrespective of the width of the range. Therefore, slopes of phase curves as shown in Fig. 5 and widths of ranges of entrainment are inversely related.

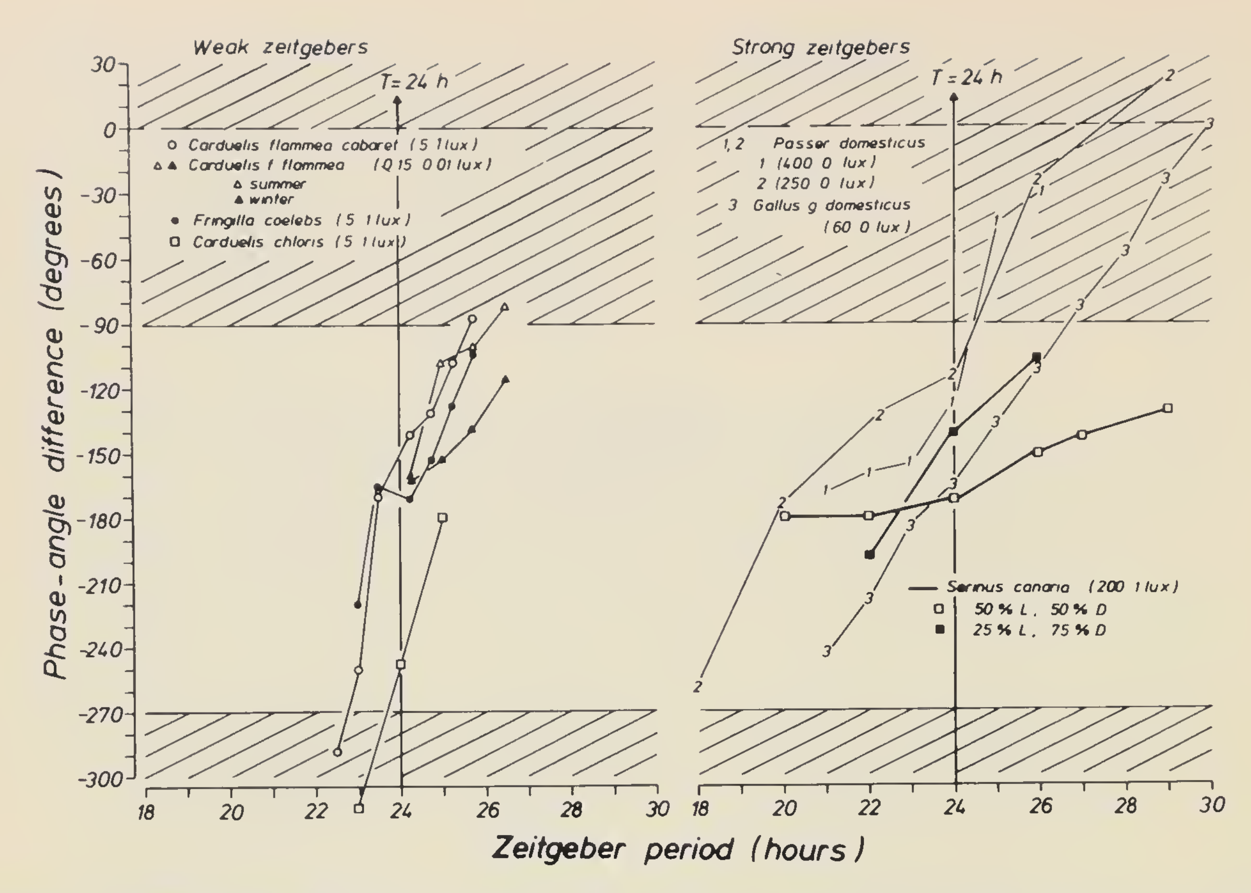


FIGURE 5. Phase-angle difference between the entrained circadian rhythm and the entraining light-dark cycle, drawn as a function of zeitgeber period T. White area: light; shaded area: darkness. Intensities of illumination during L and D given in parentheses. Data sources: ○, ●, □ ASCHOFF & POHL (1978); △, ▲ POHL (unpubl.); 1 FARNER et al. (1977); 2 ESKIN (1971); 3 MORRIS (1973).

It should be noted that in several of the experiments used to draw the phase curves of Fig. 5, the full ranges of entrainment have probably not been exploited; the difference in mean range, however, as well as the difference in mean slope between the two diagrams is representative of a variety of organisms including plants and unicellular organisms (cf. ASCHOFF & POHL, 1978). This relationship permits a quantitative estimate of the range of entrainment if the slope of the phase curve is known. Furthermore, different slopes of phase curves found in the same organism when entrained to zeitgebers of different properties indicate a difference in the strength of the zeitgeber used. An example is provided by the two phase curves for Canaries in the right diagram of Fig. 5: steeper slope of the curve obtained with the weaker zeitgeber (25% L) as compared to the curve obtained with the stronger zeitgeber (50%).

Multi-oscillator system

So far, we have treated circadian rhythms as representing (or as being driven by) one single 'master-clock'. There is, however, increasing evidence that the circadian system consists of a multiplicity of oscillators which are coupled to each other, which change their mutual phase-relationship depending on conditions, and which may become uncoupled under certain circumstances. Strong support for the hypothesis of a multi-oscillator system comes from observations of 'internal desynchronization' a state of the system in which two overt rhythms freerun with different frequencies. Internal desynchronization has been described in man (ASCHOFF et al., 1967), in the squirrel monkey *Saimiri sciureus* (SULZMAN et al., 1977), and in the ground beetle *Blaps gigas* (KÖHLER & FLEISSNER, 1978). Less

stringent but still suggestive for a multi-oscillator system are transitory states of internal dissociation among various overt rhythms that occur during reentrainment of circadian systems after phase shifts of the zeitgeber (ASCHOFF, 1978b; ASCHOFF et al., 1975). There is furthermore the phenomenon of 'splitting', i.e. the separation of an overt rhythm such as locomotor activity into two components which after transitory dissociation lock on to each other with an about 180± phase-angle difference (HOFFMANN, 1971). In birds, splitting has been observed in Starlings occurring either spontaneously or due to injections of testosterone (GWINNER, 1974).

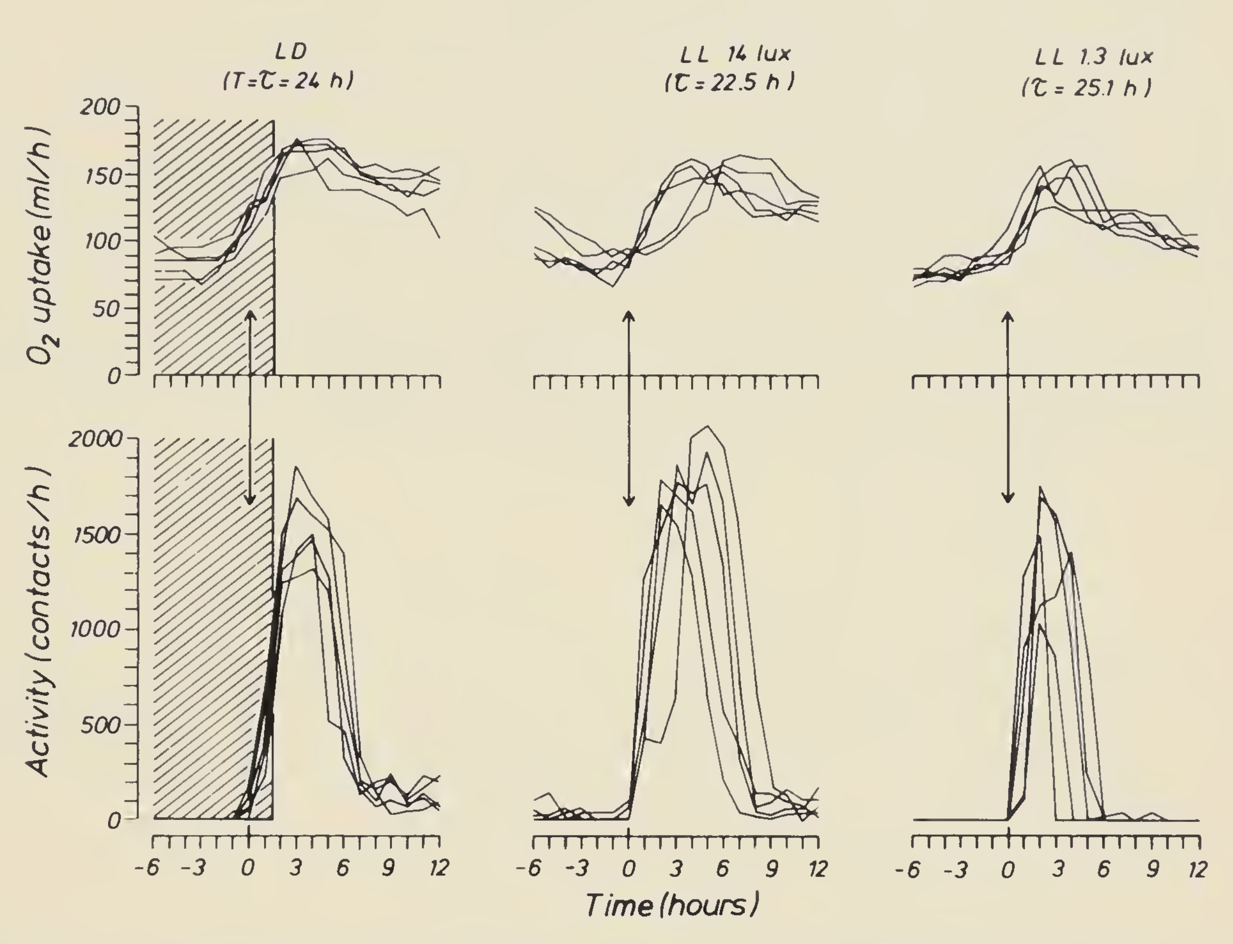


FIGURE 6. Oxygen uptake and locomotor activity in chaffinches, *Fringilla coelebs*, kept in light-dark cycles (LD) or in constant illumination (LL). In each of the three diagrams, five consecutive periods recorded in a single bird are superimposed with reference to onset of activity (= zero at the abscissa; indicated also by vertical arrows). T: zeitgeber period; τ: circadian period.

Consistent with the concept of coupled oscillators are systematic changes in the phase-relationship between rhythmic variables due to changes in the circadian period. An example of such changes in the relationship between oxygen uptake and locomotor activity is given in Fig. 6. In each diagram, 5 consecutive periods from the record of a single Chaffinch are superimposed. For entrained (left) and for freerunning rhythms (middle and right) onsets of activity are used as reference phases (= hour zero at the abscissa, indicated also by vertical arrows). In LD, oxygen uptake starts to increase about 1.5 hours prior to the onset of activity; that means the phase-angle difference ψ_{intern} between activity and oxygen uptake is -22.5°. In LL, ψ_{intern} becomes zero or slightly positive when τ is shorter than 24 hours (middle column), and it becomes more negative when τ is longer than 24 hours (right column).

Similar results have been obtained with Common Redpolls *Carduelis flammea* entrained to different zeitgeber periods. It would be premature to draw strong conclusions from measurements made in two avian species only. However, in view of similar observations made in other organisms, e.g. in mice (HAUS et al., 1967) and especially to a large extent in man (WEVER, 1972, 1973), it seems likely that changes in ψ_{intern} as a function of τ or T, respectively, are common in circadian systems. The phenomenon is mentioned in the context of this paper because similar changes occur in circannual systems (cf. Fig. 14A and B).

Apart from demonstrating changes in ψ_{intern}, Fig. 6 is of interest with regard to the often made assumption that oxygen consumption and activity are closely linked with each other, and that the rhythm of oxygen uptake is mainly, if not exclusively, the result of the rhythm of locomotor activity. Such conclusions do not take into account the fact that the rhythm of oxygen uptake can phase lead the rhythm of activity by several hours (Fig. 6), and they are incompatible with the observation that there is a rhythm of oxygen uptake in birds when they are at absolute rest because of being kept in continuous darkness. This has been shown in the Brambling *Fringilla montifringilla* (ASCHOFF & POHL, 1970a) and in the Blackbird *Turdus merula* (BIEBACH, 1974). In summary, these findings strongly contradict a simple 'cause-and-effect' relationship between the two rhythmic variables (cf. more detailed discussion in ASCHOFF, 1970; ASCHOFF & POHL, 1970b).

Properties of circannual clocks

Historical remarks

At the outset of this section, we should give credit to a few of those who, at an early stage of the game, stressed the significance of endogenous components in seasonal rhythmicity and who partly anticipated the existence of circannual rhythms. The concept has a long history, with its roots, like that of circadian rhythms, in botanical studies. (For reviews, cf. BAKER & BAKER, 1934–36; BÜNNING, 1956). In mammals and birds, the phenomena of hibernation (BERTHOLD, 1837) and migration (NAUMANN, 1822) first gave rise to speculations on internal factors governing these events. However, it was not until 100 years later that more explicit hypotheses about endogenous annual rhythms were developed.

It was the pioneer in photoperiodic control of avian reproductive cycles and migration, ROWAN, who himself advocated the idea of an internal physiological rhythm that is modified by external factors such as the varying day lengths (ROWAN, 1926). Also to be mentioned is BAKER who, in summarizing his remarkable 7 publications on seasons in a tropical rain-forest, made the distinction between 'ultimate' and 'proximate causes' for the evolution and actual timing of seasonal events (BAKER 1940–1950) – the two subjects of 'evolutionary' and 'functional' biology, respectively (MAYR, 1961). BAKER (1938) states that "there is also an internal rhythm in reproduction which may be so strong as to cause specimens of southern hemisphere birds, imported into the northern hemisphere, to continue breeding at the same time as the others of their species in the south". Later authors on the subject generally failed to notice that BAKER gave the internal rhythm enough weight to list it, in addition to light, temperature and rain, as one of the 'proximate causes'. But he also made it quite clear, with an intuitive conception of "free running"

rhythms, that other factors were indispensable to explain the temporal organization of seasonal rhythms: „Internal rhythm can never account wholly for the timing of breeding seasons, for it would get out of step with the sun in the course of the ages, but it is likely that it plays its part in making many species quick to respond to the external factors" (BAKER, 1938). More explicitely, these ideas have been developed by BAKER already in his second report from the New Hebrides (BAKER & BAKER, 1934–36), in which he discusses the analogy with a 'clock'.

Although less convinced than BAKER of an internal rhythm, LANDSBOROUGH THOMSON (1950) changed the term 'proximate (ultimate) causes' into 'proximate factors', a terminology that avoids the implication of a direct cause-and-effect relationship and allows the inclusion of zeitgebers in the class of proximate factors (IMMELMANN, 1972). At the same time, A. J. MARSHALL (1951) expressed his strong belief "that the internal gonad rhythm is the most important single factor in the timing of breeding seasons and the migration that is part of them". Ten years earlier, BLANCHARD (1941) had drawn a similar (and probably better justified) conclusion from her extensive studies of the gonadal cycle in White-crowned Sparrows *Zonotrichia leucophrys:* "It seems nearest to the truth, then, to think of the gonad cycle as the expression of an inherent annual rhythm.... which may be modified in part by environmental conditions but is by no means entirely dependent upon them for its beginning or its general subsequent course". (For a review of the earlier literature concerning this problem, cf. ASCHOFF, 1955).

Freerunning circannual rhythms

Truly circannual rhythms, persisting under seasonally constant conditions with periods different from 12 months, have first been described by PENGELLEY & FISCHER (1963) for Golden-mantled Ground Squirrels *Citellus lateralis.* For birds, circannual rhythms

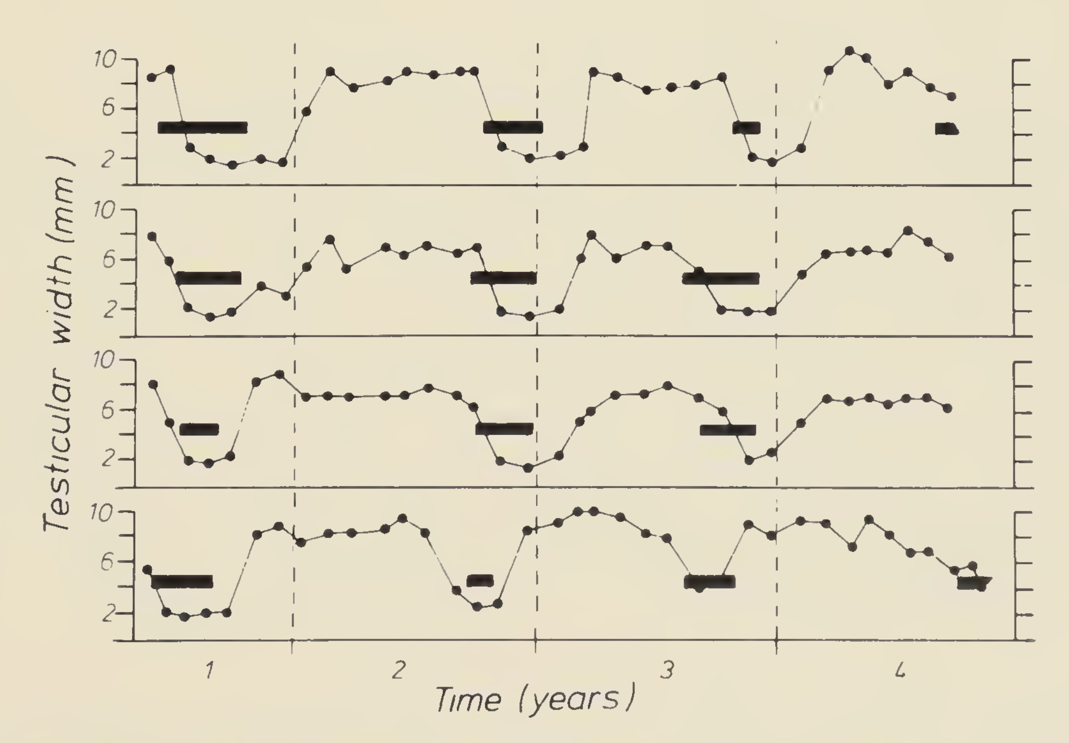


FIGURE 7. Rhythms of testicular width (curves) and moult (bars) in four selected European Starlings, *Sturnus vulgaris,* kept for 3.5 years under constant photoperiodic conditions (upper three rows: LD 11 : 11; fourth row: LD 12 : 12). (From GWINNER, 1977a).

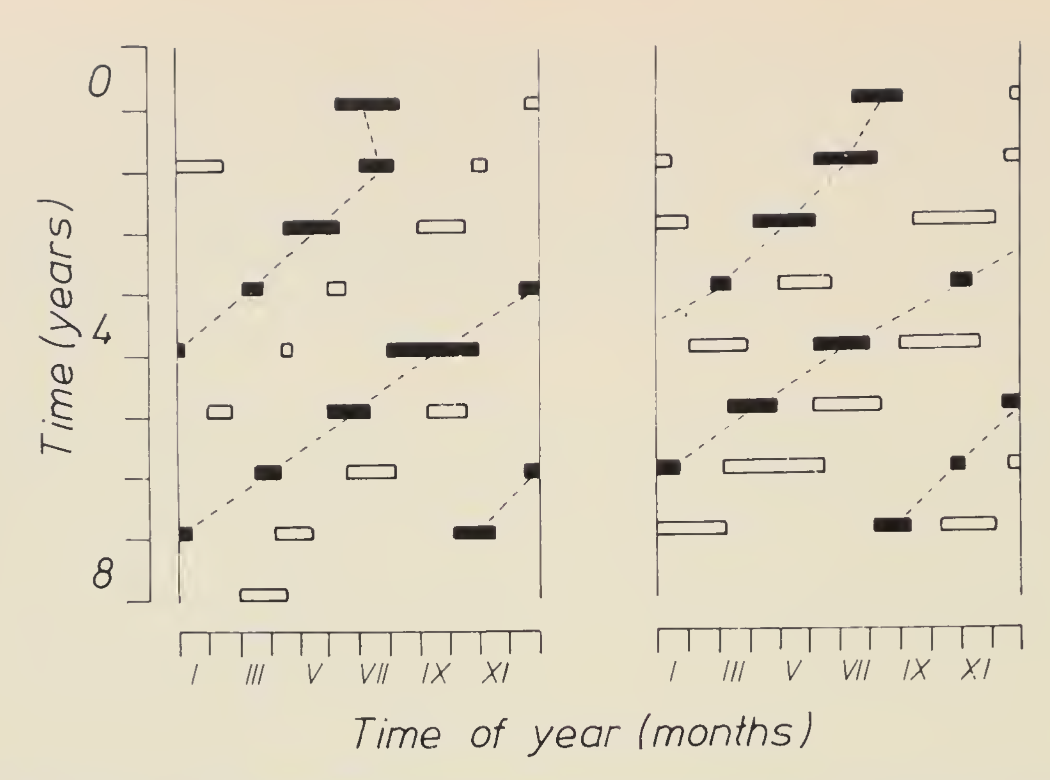


FIGURE 8. Rhythms of summer moult (black bars) and winter moult (white bars) in a Garden Warbler, *Sylvia borin,* (left) and in a Blackcap, *Sylvia atricapilla,* (right) kept for 8 years under constant photoperiodic conditions (LD 10 : 14). (From BERTHOLD, 1978).

freerunning over more than two cycles were demonstrated in Willow Warblers *Phylloscopustrochilus* by GWINNER (1967, 1968), in Garden Warblers *Sylvia borin* and Blackcaps *Sylvia atricapilla* by BERTHOLD et al. (1971, 1972 a, b), and in European Starlings *Sturnus vulgaris* by SCHWAB (1971). These birds had been kept in LD-cycles with T = 24 h but with various photoperiods (LD 12 : 12, 10 : 14, 14 : 10 and 16 : 8 respectively). The data shown in Fig. 7 are from an experiment in which European Starlings were kept in constant conditions of temperature and photoperiod for 3.5 years (GWINNER, 1977 a). The undamped oscillations in testicular width and the intervals between successive moults deviate from 12 months. The deviation of the circannual period is more conspicuous in Fig. 8 which presents data on moult from two warblers kept in LD 10 : 14 for 8 years (BERTHOLD 1978). In consecutive years, summer moult (black bars) and winter moult (white bars) occur progressively earlier; the resulting freerunning rhythms, indicated by dashed lines, have mean periods of about ten months.

In the meantime, circannual rhythms freerunning in LD for at least two cycles have been demonstrated in at least 10 species of birds; results from some 10 others are suggestive (GWINNER, 1975; BERTHOLD, 1979). Most of these experiments have been carried out in conditions of constant light-dark cycles. However, circannual rhythms have also been demonstrated under conditions of continuous light or darkness (cf. the review in GWINNER, 1979). The longest records, showing regularily recurring cycles of testicular growth and regression are those obtained from Pekin ducks kept in DD for 70 months (BENOIT et al., 1956, 1970).

It has been argued that animals that are kept under conditions of constant photoperiod, e.g. in LD 12 : 12, are not exposed to truly 'constant' conditions, and hence that those experiments are not apt to solve "the problem of separating, experimentally, any endogenous contribution to the timing of cycles from strong, and perhaps overriding

physiological reactions to the photoperiod itself" (Sansum & King, 1976). In the opinion of these authors, experiments are to be made in LL or DD to really prove an 'endogenous' annual rhythm (King 1968, Hamner, 1971). In discussing these criticisms one has to distinguish among several hypotheses that are not always clearly separated in the publications of those arguing against the endogenous nature of 'circannual' rhythms.

(1) The LD-cycle might represent a periodic input (a 24-h input) into the system generating (via frequency transformation) an output with a period of about 365 days. Sensu stricto, such a model of a 1 : 365 ratio in frequencies implies that the circannual τ is positively correlated with (and proportional to) the period T of the LD-cycle. Unpublished data from Gwinner disagree with this prediction from the model in so far as European Starlings, kept in LD-cycles with T = 22 h (LD 11 : 11) tended to have circannual rhythms with τ-values similar to or even slightly longer (instead of shorter) than those of conspecifics kept in T = 24 h (LD 12 : 12) Apart from this direct experimental evidence against it, several phenomena are extremely difficult to reconcile with this model. For instance, it is hard to see how this model copes with the facts that individual birds exposed to the same LD conditions can produce quite different circannual τ-values, and that during exposure to a constant photoperiod, e.g. LD 10 : 14, the period of the freerunning circannual rhythm may be longer than 12 months at the beginning and shorter than 12 months later on (cf. Fig. 8, left diagram). Still stronger arguments against this hypothesis come from experiments demonstrating the entrainability of circannual rhythms by photoperiodic cycles differing from 12 months (cf. the following section).

(2) Instead of being a causal stimulus generating circannual rhythms, the 24-h light-dark cycle might represent a zeitgeber that entrains an annual rhythm by frequency-demultiplication – similar to the entrainment of a circadian rhythm by a high frequency LD-cycle, e.g. LD 2 : 2 (Bruce, 1960). This model presupposes the existence of an endogenous rhythm that can be entrained, and hence cannot be used as an argument against self-sustaining circannual rhythms.

(3) Besides hypothesis (1) and (2), circannual rhythmicity might be based on a mechanism that counts about 365 revolutions of the circadian clock. Again, this model is not an alternative to the 'endogenous' circannual concept but rather proposes a specific process generating circannual rhythms. It predicts a positive correlation between the circadian and the circannual τ. To test the hypothesis, and to separate it from the generating process discussed above as hypothesis 1 (counting external days), organisms must be kept in LL or in DD. Such experiments have been performed by Gwinner (1973) with European Starlings, kept for 15 months in LL with an intensity of illumination of 0.7 lux. In the 9 birds tested, the circadian periods varied from 22.5 to 24.2 hours, and the circannual periods form 10.6 to 13.8 months. There was a weak positive correlation between the two sets of data (significant at the 5% level), but the regression line was 2.4 times steeper than the (model predicted) 1 : 1 ratio between circadian and circannual periods. Gwinner (1973) concludes from these results that "circadian and circannual rhythms are apparently not entirely independent of each other. Whether the positive correlation between the periods of the two rhythms reflects a causal relationship between the two periodicities or rather a common dependence of both rhythms on other factors remains to be seen". The results from experiments with entrainment of the circadian

system to different T-values, mentioned under (1), clearly contradict the hypothesis that circannual rhythms are the product of 'counting' 365 circadian revolutions.

(4) The LD-cycle has been considered a constant stimulus to which the biological system responds alternatively in two opposite ways. According to this concept, a photo-regime of LD 12 : 12 (a photoperiod close to the photoperiodic response-threshold of many species) "appears to be short enough to allow the 'breaking' or dissipation of refractoriness, yet it is long enough to provide photostimulation once the birds become photosensitive" (Sansum & King, 1976). Whereas this model, once again, proposes a theoretically feasible mechanism underlying circannual rhythms, it cannot be regarded an alternative of circannual rhythms. Such an interpretation would neglect the fact that the necessary alternations in responsiveness to one and the same, all year round unchanged stimulus occur spontaneously (i.e. without a change in environmental conditions) within the organism. Regular switches between two states during which the system responds differently to a constant stimulus, represent an 'oscillation' that is 'endogenous' by definition because it is not triggered by periodic changes in the environment. In fact, a changing responsiveness to a constant environmental stimulus is a characteristic of all circa rhythms (Aschoff, 1960). To conclude from the changing interaction between stimulus and system that the rhythm is driven 'exogenously', is a reasoning similar to the concept of 'autophasing' (in its first version) as it was developed by Brown (1959, p. 1542) for the circadian system to explain the freerunning circadian rhythm in LL as a repetition of 'responses' to the light stimulus (cf. the discussion in Aschoff, 1963). While rejecting hypotheses 1 to 4, as well as the demand for experiments in LL or DD, we fully agree that the permissive conditions, including photoperiods, under which circannual rhythms can be observed, need exploitation. As for circadian rhythms, we have to expect circannual rhythms to operate within certain limits of conditions only. It is puzzling but not too surprising that some species seem to exhibit circannual rhythms in LD 12 : 12 but not in longer and shorter photoperiods (Schwab, 1971) while others show circannual rhythms either in long or in short days but not under LD 12 : 12 conditions (Goss, 1969a). To find out when and how the system oscillates, and under what conditions the system fails to oscillate, will be one of the tools to disentangle the physiological mechanisms underlying annual periodicity and its control by photoperiod, including concepts such as external versus internal coincidence (Pittendrigh, 1972, 1974). Under this point of view, the search for inductive external factors (as in most photoperiodic studies) is turned into a search for 'inhibitors' (Marshall, 1960) that depress and hence delay the spontaneous course of the internal rhythm.

Entrainment by zeitgebers

If freerunning circannual rhythms represent, in analogy to circadian rhythms, self-sustaining oscillations, it is to be expected that entrainment of these rhythms by zeitgebers follows the rules outlined in the first section (cf. especially Fig. 2). In view of the drastic effects of photoperiod on seasonal phenomena (Farner & Lewis, 1971; Farner & Follett, 1979), a periodically varying photoperiod is the obvious candidate for a zeitgeber. In the following discussion we mainly concentrate on a set of data obtained by Gwinner (1977 b, c, and unpublished) from European Starlings. Five groups of 8 to 12 birds each were exposed to artificial LD-cycles with sinusoidal changes in photoperiod

(longest day: 15 h L, shortest day: 9 h L; no twilights). Amplitude and general shape of these photoperiodic cycles were the same for all groups, but their duration varied from 1 cycle per year to 4 cycles per year, representing zeitgeber periods of 12, 8, 6, 4 and 3 months respectively. In each bird, testicular width was established at 2- to 4-week intervals by laparotomy, and body weight was measured at the same times to the nearest 0.1 g; onset and end of moult were determined by frequent inspection with a possible error of ± 2 days. The results on testicular cyles are summarized in Fig. 9. In analogy with the presentation of circadian entrainment data, the zeitgeber is indicated by an alternation of shaded areas (photoperiod below 12 hours) and white areas (photoperiod above 12 hours). Testicular cycles are clearly expressed under all five conditions, and the cycles are in synchrony with all 5 zeitgeber frequencies.

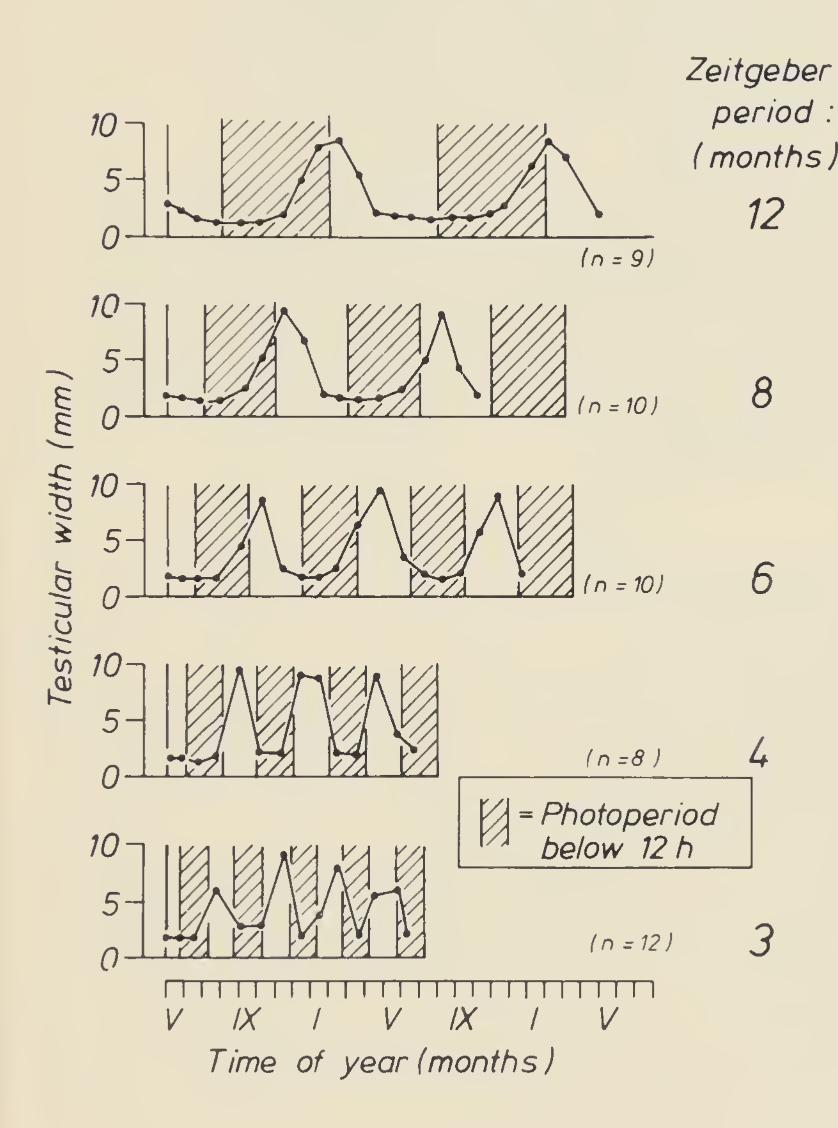


FIGURE 9. Rhythms of testicular width in five groups of European Starlings, *Sturnus vulgaris,* kept in light-dark cycles with periodically varying photoperiods. Duration of the photoperiodic cycle indicated at the right margin. Each curve represents the mean of n animals. Shaded area: Photoperiod below 12 h, white area: photoperiod above 12 h. (After GWINNER 1977b).

In Fig. 10, consecutive cycles in testicular widths have been superimposed on each other for each of the five zeitgeber periods (upper row). In addition, the figure shows the cycles in body weight (lower row) and the duration of moult (black bars in the middle row). In all diagrams, the shortest day (= zero at the abscissa; vertical dashed line) is used as a reference phase of the zeitgeber. Again, the shaded areas represent the 'winter half year' (photoperiod below 12 h) and the white areas the 'summer half year' (photoperiod above 12 h). The following conclusions can be drawn: a) testicular cycles and moult follow all zeitgeber periods, but changes in body weight become rather irregular in T = 3 months; b)

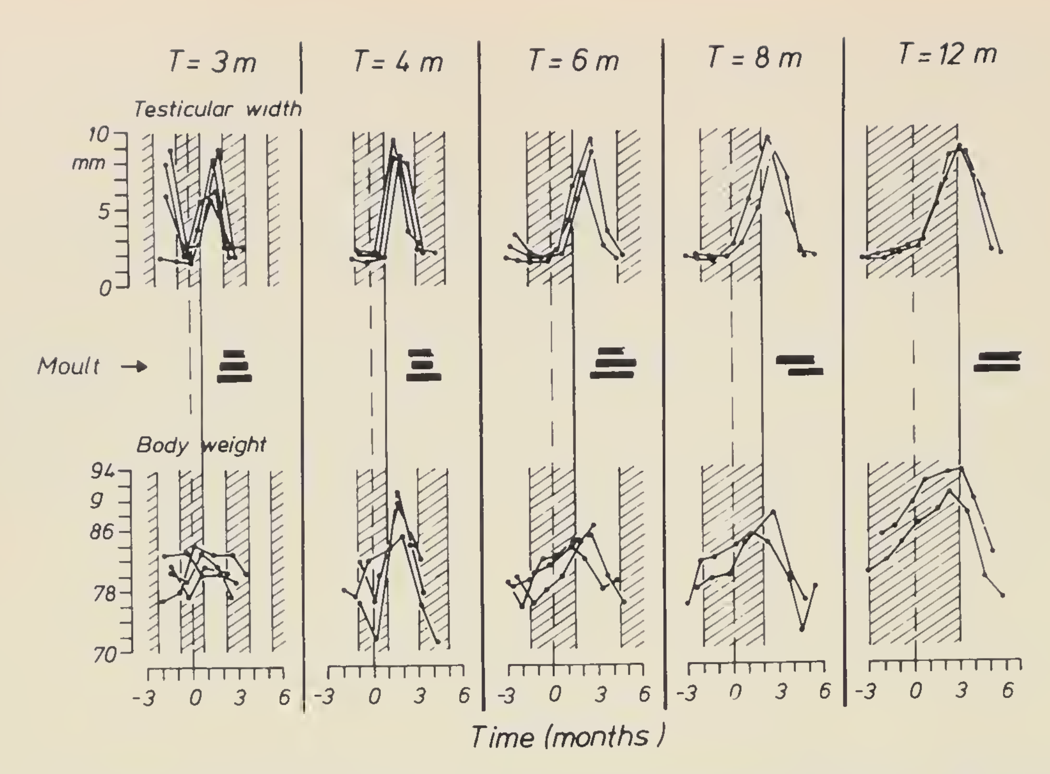


FIGURE 10. Rhythms of testicular width (above) and of body weight (below) together with times of moult (bars) in five groups of European Starlings, *Sturnus vulgaris,* kept in light-dark cycles with periodically varying photoperiods (zeitgeber period T = duration of the photoperiodic cycle in months). Curves represent mean values from 8 to 12 animals of each of the 5 groups: consecutive periods are superimposed with reference to the shortest day (vertical dashed line). Shaded area: photoperiod below 12h; white area: photoperiod above 12h. (After GWINNER 1977b, and unpublished).

the phase-angle difference between cycles and zeitgeber as well as among various cyclic variables change as the zeitgeber period is shortened. To demonstrate this latter effect more clearly, mean patterns of all three variables are drawn in Fig. 11 as a function of the zeitgeber period expressed now in degrees instead of in hours. Zero degree at the abscissa represents the shortest day (vertical dashed line). As reference phases for testicular width (closed circles) and body weight (open circles) we have computed 'centers of gravity', using the maximal value in each curve and its two neighbouring values. These centers are indicated in Fig. 11 by black arrows (testicular width) and white arrows (body weight). From the top to the bottom of Fig. 11, i.e. from long to short zeitgeber periods, the arrows as well as the black bars indicating moult move progressively to the right, i.e. to later phases of the zeitgeber. With regard to the phase-relationship between rhythm and zeitgeber, this means a steady decrease in external phase-angle differences from long to short zeitgeber periods. In addition, the interval between either arrow and black bar increases, on the average, from top to bottom, indicating an increase in internal phase-angle difference between moult and the two other variables (cf. Fig. 14).

In Fig. 11, the presentation of data in reference to degrees of a full zeitgeber period is useful in demonstrating phase relationships, but it obscures the relations in absolute time, especially the 'compression' of the biological cycles or parts of them due to the shortening of the zeitgeber period. This is shown in diagram A of Fig. 12 for moult and for that part of the gonadal cycle during which the testes are wider than 4 mm ('large testes'). When entrained to a zeitgeber period of 12 months testes are large for nearly 4 months, and moult lasts for 3 months, i.e. for 32% and 25% of the full cycle, respectively (cf. diagram B in

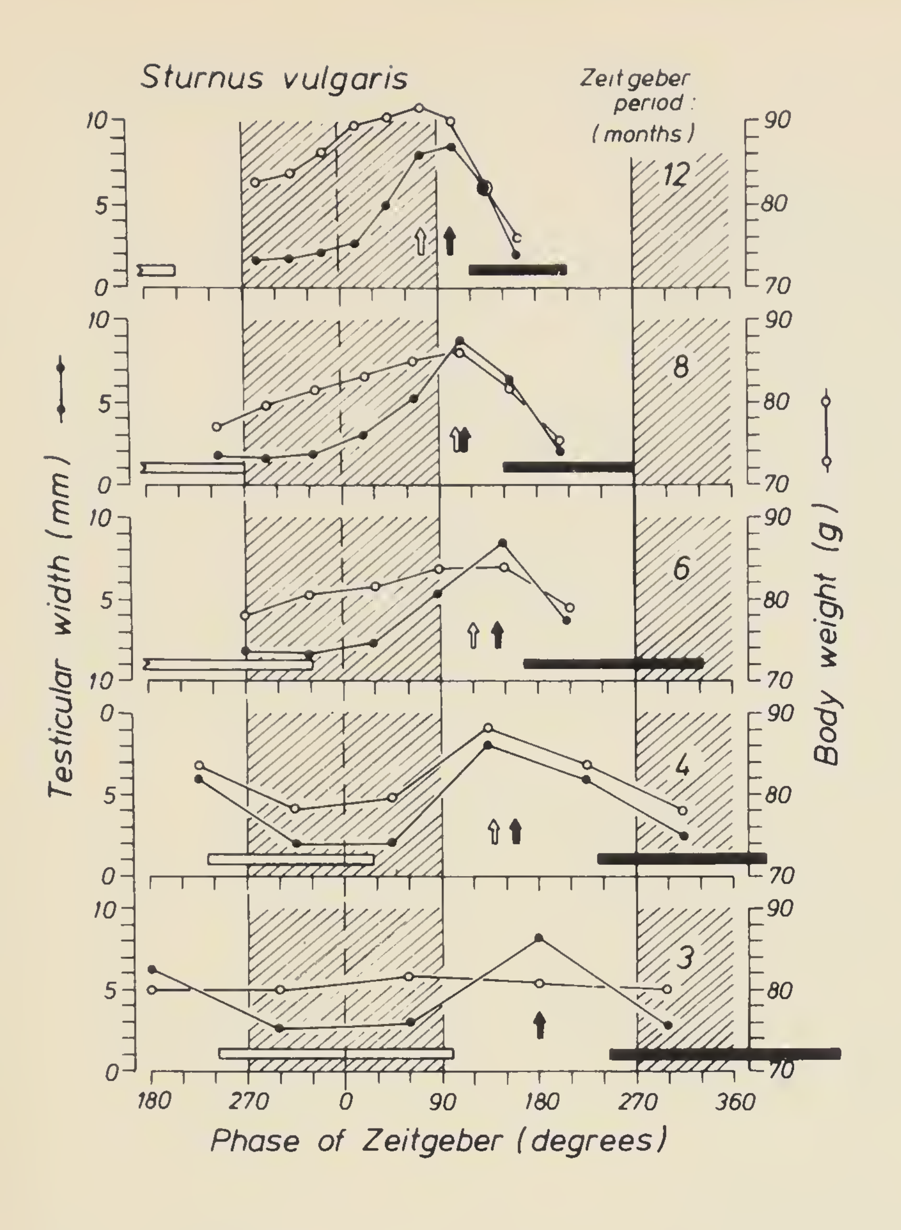


FIGURE 11. Rhythms of testicular width (closed circles), body weight (open circles) and moult (bars) in five groups of European Starlings, *Sturnus vulgaris*, kept in light-dark cycles with periodically varying photoperiods. Duration of the photoperiodic cycle indicated on the right side of each diagram. Mean pattern of several cycles drawn with reference to the phase of the zeitgeber (zero degree = shortest day). Shaded area: photoperiod below 12 h; white area: photoperiod above 12 h. Arrows: Centers of gravity around the maxima of testicular width (black) and body weight (white) (After GWINNER 1977b, and unpublished).

Fig. 12). With T = 3 months, these two time spans are reduced to 1.5 and 1.7 months, respectively. Despite this drastic 'compression', the times of large testes and of moult now encompass more than 50% of the full cycle (diagram B). In other words, the times allocated for the less 'active' states (i.e. times of small testes and non-moult) which occupy more than 8 months in T = 12 months, are reduced to about 1.5 months in T = 3 months. Hence, the average reduction is 58% for the more 'active' states, but 82% for the less 'active' states. Another interesting aspect concerns the time during which testes are still large while moult is already in progress. This 'overlap' (diagram C in Fig. 12) amounts to 1 month in T = 12 months and decreases to 0.3 month in T = 3 months; in percent of the full cycle, the overlap remains nearly constant in all zeitgeber periods (diagram D in Fig. 12).

In summary, these data demonstrate the entrainability of circannual rhythms by photoperiodic zeitgebers and further changes in external phase-angle difference that agree with expectations made on the basis of oscillation theory, and that correspond to the situation in circadian rhythms. Moreover, there seems to be less 'compressibility' for 'active' states as compared to 'inactive' states of the cycles, and less compressibility for moult than for the time of large testes (cf. the two lines in diagram A of Fig. 12). Finally, cycles of moult and testicular width are still clearly entrained to T = 3 months while entrainment of the body weight rhythm is questionable. This latter observation might suggest different ranges of entrainment for different variables, a problem that is discussed in more detail in the following section.

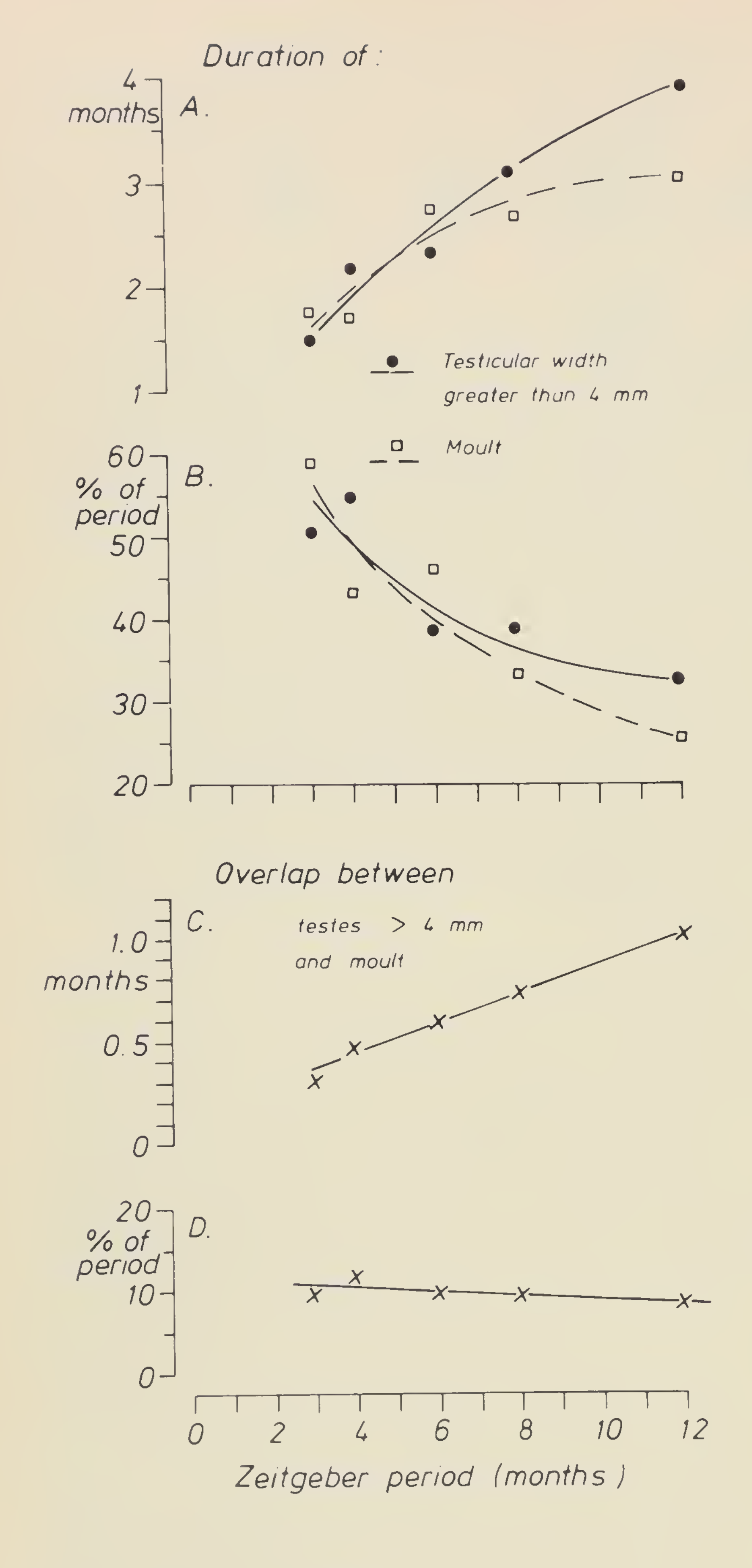


FIGURE 12. Circannual rhythms of testicular width and moult in European Starlings, *Sturnus vulgaris*, entrained by photoperiodic zeitgebers. Duration of moult and of the time during which testes are large (A,B), and duration of the overlap between these two time spans (C), drawn as function of zeitgeber period. (After GWINNER 1977b).

Ranges of entrainment

As has been shown earlier, avian circadian rhythms have ranges of entrainment that are relatively small. Even with strong zeitgebers, they rarely encompass more than 10 h, i.e. about 40% of the 'natural' period. For circannual rhythms, the range seems to be surprisingly large. Most certainly, the 9 months indicated by the Starling data do not represent the full range. For the testicular cycle, we have data suggesting entrainment even

to a zeitgeber period of 2.4 and 2 months. These results have not been included here because at very short periods the determination of phase-angles becomes difficult because not enough values can be obtained within one cycle. In addition, as changes in phase become less distinct, it also becomes more difficult to separate masking effects from true entrainment. Hence, there is uncertainty about the lower limit of the range of entrainment. The same is true for the upper limit, because no experiments have been made so far with zeitgeber periods longer than 12 months. In conclusion, the full range of entrainment for Starlings may very well extend over 20 or even more months, i.e. to twice the 'natural' periods. Is such a range too large to be considered compatible with the characteristics of a self-sustaining oscillation?

In trying to answer this question, we first note that there are circadian systems that have quite large ranges of entrainment. A few examples are provided in diagram B of Fig. 13 which are presented in the same manner as the two diagrams in Fig. 5. The phase curve No. 1 is the same as that shown by open circles in the left diagram of Fig. 5 (Lesser

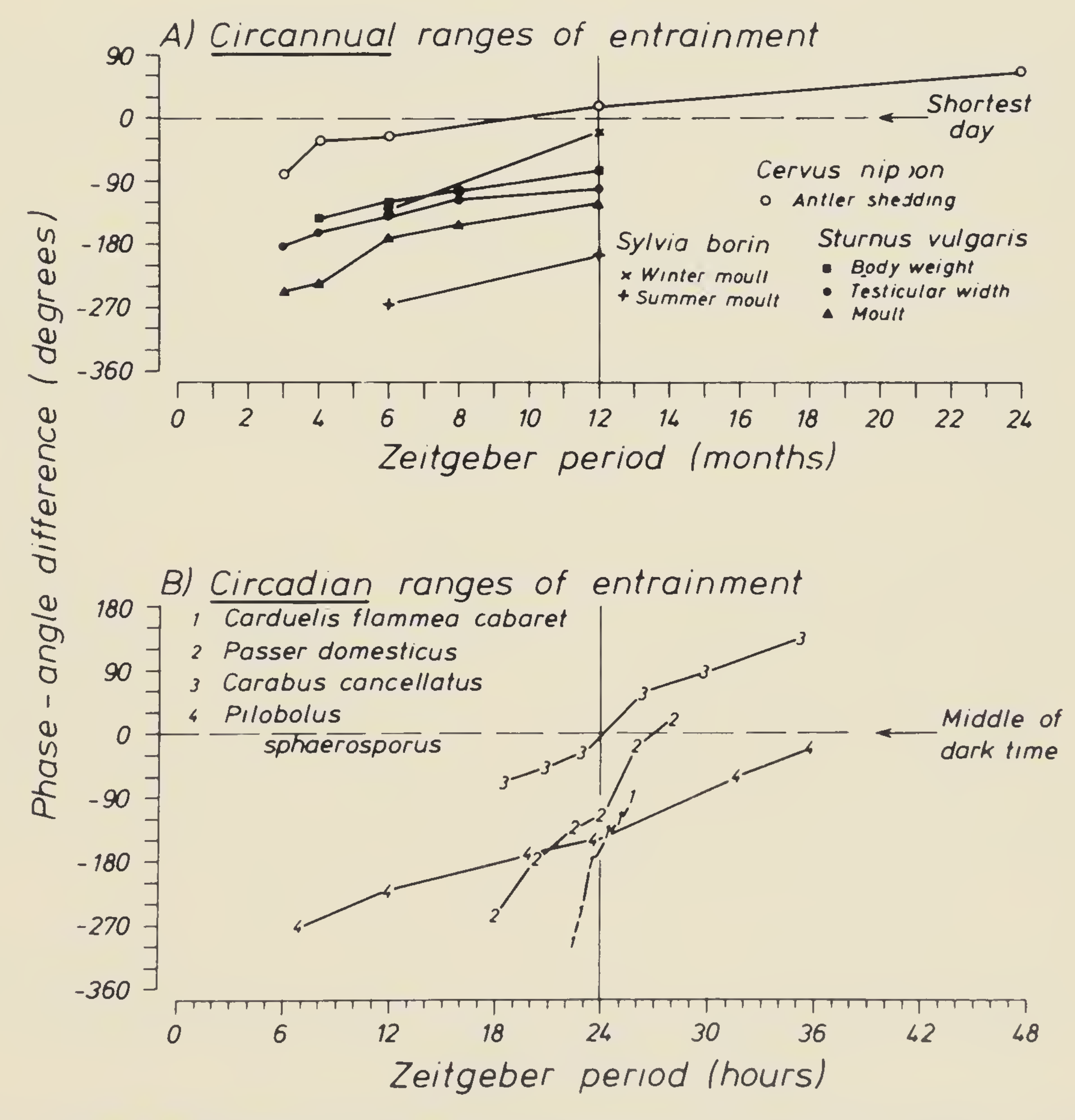


Figure 13. Phase-angle differences between circannual (A) and circadian (B) rhythms, respectively, and the entraining zeitgeber (periodically varying photoperiod for A, constant light-dark cycle for B). Data sources: O sika deer (Goss, 1969b); ●, Δ, ■ European Starling (Gwinner, 1977c); ×, + Garden Warbler (Berthold, unpubl.); 1, Lesser Redpoll; 2, House Sparrow; 3, ground beetle; 4, mold (from Aschoff & Pohl, 1978).

Redpoll), and curve No. 2 the same as curve No. 2 in the right diagram of Fig. 5 (sparrow). Phase curve No. 3 (ground beetle) is typical for several insect species, and curve No. 4 (mold) typical for serveral plant species (cf. Fig. 2 in ASCHOFF & POHL, 1978). The diagram indicates, first, large differences in the widths of ranges of entrainment, and, secondly, demonstrates again the inverse relationship between the width of the range of entrainment and the slope of the phase curve. The curve for the House Sparrow (No. 2) represents a change in phase-angle difference of 27° per 1 h change in period; the range is 10 h. The curve for the mold (No. 4) represents a change of 9° per 1 h change of period, and the range is 30 h. In other words: with a slope one third as steep the range of entrainment is three times as large.

On the assumption that similar principles apply to the entrainment of circannual rhythms as to the entrainment of circadian rhythms, it seems justified to predict a range of entrainment for circannual rhythms from the slope of their phase curves. Such phase curves are presented in diagram A of Fig. 13. Curves connecting closed symbols will be considered first. They represent data from experiments made with birds, and they all have more or less the same slope of about 12° change in phase-angle difference per 1 month change in zeitgeber period. This corresponds to 6° change per 15° in period. The circadian phase curve of the House Sparrow (No. 2 in diagram B) has a slope of 27° per 15° change in zeitgeber period, that means the slope of the circadian phase curve is 4.5 times steeper than the slope of the circannual phase curve. From this we predict that the range of entrainment for the circannual rhythm will be 4.5 times larger than the circadian range. The circadian range is 10 hours, i.e. 41.5% of 24 h. The circannual range is expected to be 4.5 times larger, that is 4.5 x 41.5% = 187% of 12 months. The prediction then is that circannual rhythms of birds whose phase curves have a slope of 12° per 1 month change in period, may have ranges of entrainment not too far from 22.5 months. If a zeitgeber period of 2 months represents the lower limit of this range, the upper limit can be expected to be close to 24 months.

The only species in which the full range of entrainment for circannual rhythms has been exploited is the Sika Deer *Cervus nippon*. GOSS (1969b) was successful in synchronizing the rhythm of antler shedding to periodically changing photoperiods with T-values varying from 3 to 24 months. A zeitgeber period of two months was clearly below the range of entrainment because all animals tested became entrained via frequency demultiplication in a 1 : 6 ratio. With T = 24 months, only 2 out of the 5 animals were entrained in a 1 : 1 ratio, whereas the other 3 went through two cycles in 24 months (= 2 : 1 ratio), indicating that they were beyond their range of entrainment. The phase curves derived from the data of GOSS are shown in Fig. 13 (diagram A, open circles).

In discussing ranges of entrainment, one must bear in mind that the circannual system may represent a system of several coupled oscillators as does the circadian system. There is good evidence, for the circadian system, that ranges of entrainment differ among variables, indicating differences in the 'degree of persistence' among oscillators (ASCHOFF, 1978a). It is likely that such differences in entrainability apply to circannual rhythms as well. Support for this hypothesis comes from the observation in Starlings that the rhythm in body weight becomes irregular in T = 3 months when the testicular cycle is still clearly expressed (cf. Fig. 10 and 11). It has been shown further that, under some seasonally constant conditions, some variables may and others may not show freerunning circannual rhythms

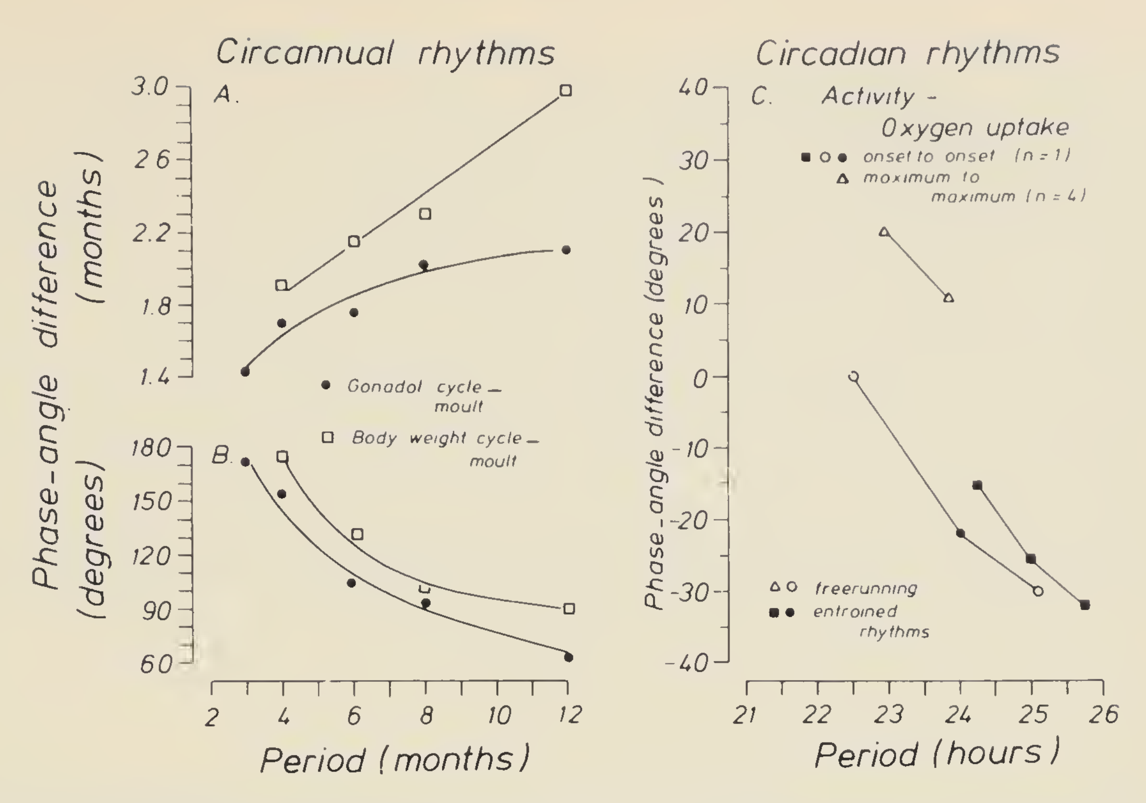


Figure 14. Internal phase-angle differences between two rhythmic variables in circannual (A and B) and in circadian systems C). A and B: European Starlings, *Sturnus vulgaris* (Gwinner, 1977b, and unpubl.). C. ○, ●, △ Chaffinch, *Fringilla coelebs* (Pohl, 1971 and data from Fig. 6); ■ Common Redpoll, *Carduelis f. flammea* (Pohl, unpubl.).

indicating differences in 'permissive' conditions for various functions. Finally, changes in internal phase-angle difference can be quoted in support of a multi-oscillator system. In the Starling, such changes are conspicuous, at least between moult on the one hand and the cycles of body weight and testicular width on the other hand (cf. Fig. 11). The phase-angle differences among these variables, measured between 'centers of gravity' and middle of moult, are given in actual time (months) in diagram A of Fig. 14. In T = 12 months, the cycles of testicular width and of body weight phase lead moult by 2.1 and 3 months, respectively; in T = 4 months, the phase lead is reduced to 1.7 and 1.9 months, respectively. Expressed in degrees (diagram B), the phase-angle differences increase from less than 90° in T = 12 to nearly 180° in T = 4. It is of interes to compare these relative changes with the changes that occur in circadian systems when T or τ is changed. Data from a few experiments are summarized in diagram C of Fig. 14. The coordinates used for diagram C are both stretched in linear proportion to those of diagram B; hence, the slopes of the curves can be compared. For a 10% change in period, internal phase-angle differences change by about 30° among circadian rhythms, but only by about 10% among circannual rhythms. This again reflects the difference in ranges of entrainment between circadian and circannual systems. Together with the systematic changes in 'overlap' between moult and large testes (cf. Fig. 12), the observations just mentioned must be taken as a warning against concepts that assume direct 'cause-and-effect' relationship between various annual cycles or that are restricted to strongly bound 'sequences of events' (see Mrosovsky, 1970).

At the present time, no definite answers can be given to the questions of the extent to which various annual cycles are interdependent on each other, of the number of circannual oscillators to which they are coupled, and whether they react differently to a varying

photoperiod or other zeitgebers (cf. the following section). Results obtained from Old World warblers suggest a high degree of independence among several events (e.g. moult, zugunruhe, fattening and gonadal size) which, when freerunning in constant conditions, have been found to change their internal phase-relationships by many months (GWINNER, 1968; BERTHOLD et al., 1972 a, b). Once more it seems appropriate to refer to BLANCHARD. In her paper published with ERICKSON (1949), when discussing the 'sequence of causation' for gonadal cycles, moult, fat deposition and migration, she states: "Therefore the obvious working hypothesis is that these changes have developed in some degree interdependently, and that the earliest appearance of any part of the pattern is to be taken as the initiation of an adjusted and coherent whole. It must, however, always be admitted that gonad changes might be a separate element dependent on the inherent cycle or on its own set of environmental factors, while other subsequent elements might, at their own time, respond to different internal or external stimuli."

Photoperiod: cause of cycles or zeitgeber?

The data discussed in the foregoing sections support the hypothesis that a periodically varying photoperiod acts as an entraining zeitgeber on circannual rhythms. This view is supported by the systematic changes in phase-angle difference due to changes in zeitgeber

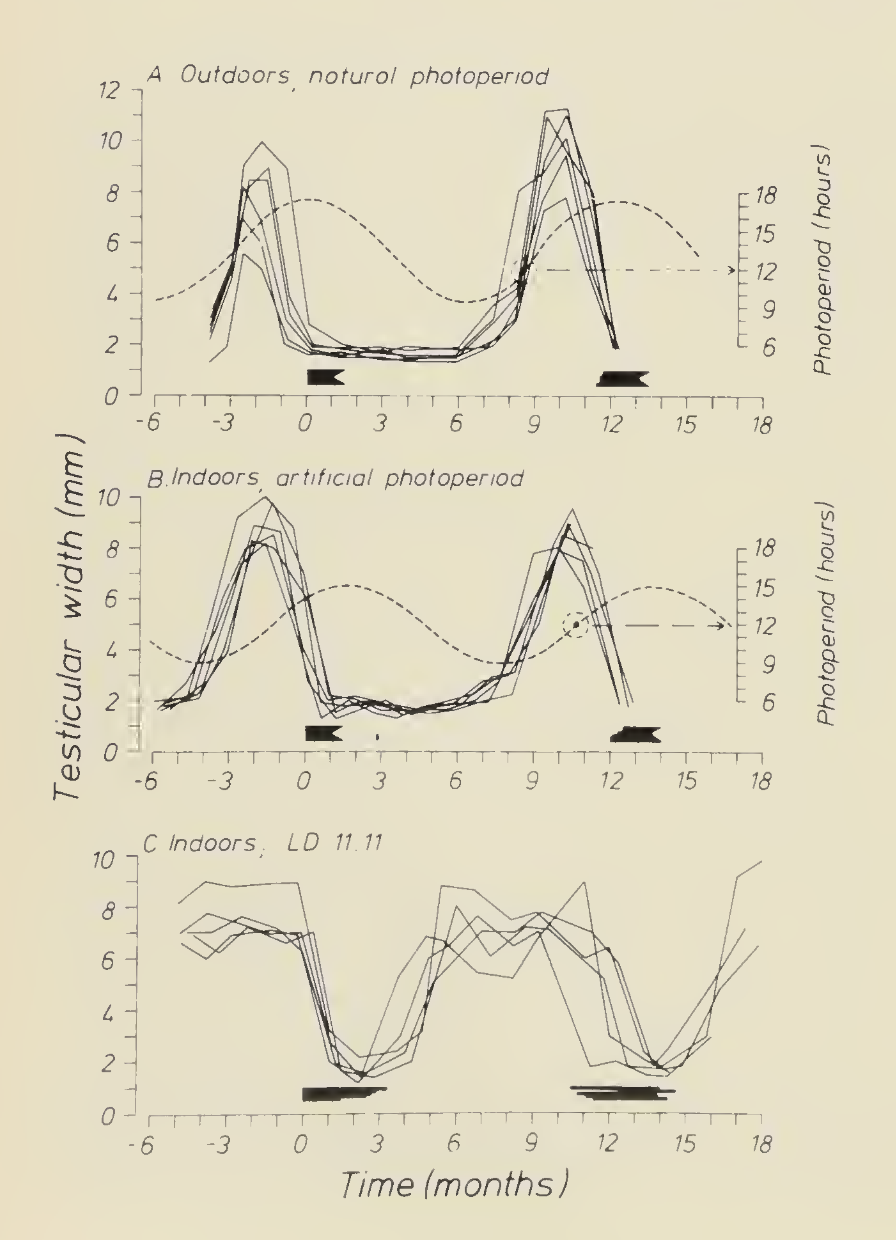


FIGURE 15. Rhythms of testicular width (solid curves) and moult (black bars) in three groups of European Starlings, *Sturnus vulgaris*. Data from six (A and B) or five selected individuals (C), respectively, are drawn with reference to onset of moult in the first year (zero at the abscisse A). Birds kept outdoors in aviaries at 48° northern latitude; B) Birds exposed indoors to a periodically varying photoperiodic simulating conditions at about 40° latitude; C) Birds exposed indoors to a constant lightdark cycle (LD 11 : 11). In A and B, photoperiods indicated by dashed curves (circles around L ° 12 h).

period (cf. Fig. 11 and 13). Further evidence is provided in Fig. 15 in which testicular cycles are compared from three groups of European Starlings: group A kept outdoors in aviaries and hence exposed not only to the natural photoperiod (including twilights; dashed lines) but also to changing temperatures and other weather conditions; group B kept indoors at a constant temperature of about 20° and exposed to a periodically varying artificial photoperiod (dashed line); group C kept indoors at 20° and exposed to a constant LD 11 : 11. For each group, testicular widths of six birds (A and B) or five birds (C), respectively, are drawn (solid lines) together with the times of moult (black bars). Onset of moult in the first year is used as a reference phase for all curves (= zero at the abscissa).

Table 1: Temporal parameters of testicular cycles and their external as well as internal phase relationships in three groups of European Starlings, *Sturnus vulgaris*, kept outdoors (A), indoors under a periodically varying photoperiod (B), and indoors under a constant light-dark cycle LD 11 : 11 (C)

	Group A	Group B	Group C
I. Duration of time (months) during which the testes are wider than 6 mm	2.4	2.6	5.5
smaller than 3 mm	8.4	7.5	3.0
II. Range of oscillation (mm) of the rhythm in testicular width (mean of 2 cycles)	7.5	7.2	6.3
III. Width of testes (mm) at the onset of moult (mean of 2 cycles)	3.4	4.0	6.4
IV. Width of testes (mm) when the photoperiod reaches 12 h in 'spring'	6.0 *	7.9 **	
V. Months after (−) or before (+) the shortest day when testes surpass a width of 2 mm	−0.6	+1.2	

* still growing ** already regressing

Most striking are the differences in pattern between group C and the other groups. The freerunning rhythms of testicular width have long lasting 'plateaus' of large testes and only a short time span during which the testes are regressed. Contrary to this picture, in both groups of entrained Starlings the testes reach maximal values for a short while only, but remain at their quiescent state for several months. In Table 1, figures describing these differences are given in row 1. The range of oscillation in testicular widths is about 17%larger in groups A and B than in group C (row II). There are also differences in size of testes at the onset of moult: in group A, the testes are more or less regressed when moult starts, while in group C they still have their maximal size at that time (Table 1, row III). Furthermore, recrudescence of testes begins several months after moult is finished in group A and B (not to be seen in Fig. 15), but already at the end of moult or somewhat earlier in group C.

In summary, the entrained rhythms differ from the freerunning rhythms in 'amplitude', in wave form, and in the phase-relationship between the rhythms of testicular width and of moult. It is not difficult to interpret these differences as a combination of phase controlling and of masking effects of the zeitgebers in Groups A and B.

Differences between group A and group B concern especially the phase-relationships between the biological rhythms and the varying photoperiod. According to row IV of Table 1, the testes in group A have reached an average width of 6.0 mm when the increasing photoperiod surpasses 12 h (indicated in Fig. 15 by a dashed circle). At the same photoperiod, the testes in group B have already begun to regress but are still 30% wider than those in group A. Recrudescence of testes starts much earlier in group B than in group A. In both groups, the testes are below 2 mm for several months; they surpass a width of 2 mm 0.6 months after the shortest day in group A, but 1.2 months before the shortest day in group B (Table 1, row V).

The differences observed between groups A and B are well compatible with, if not demanded by, the hypothesis that circannual rhythms are entrained by zeitgebers. Group B is exposed to only one zeitgeber, the periodically varying photoperiod. Contrary to this, for group A the natural environment provides not only a photoperiodic zeitgeber of larger 'amplitude' (about 7.5 h as compared to 6 h for group B) but most probably additional zeitgebers such as cycles in ambient temperature. From the difference in strength of the zeitgebers, a difference in the phase-relationship between rhythm and zeitgeber, corresponding to comparable findings in circadian rhythms, can be expected. Since in Starlings, the circannual τ is shorter than 12 months (Schwab 1971; Gwinner, unpubl.), the weaker zeitgeber results in a more positive (less negative) phase-angle difference for group B as compared to group A (cf. Table 1, row V). It might be that these differences can also be accounted for by the concept of an entirely external photoperiodic control, but probably not without the introduction of several ad hoc assumptions.

In summary, the demonstration of freerunning rhythms together with the observation that the system, when exposed to periodically changing environmental factors, shows all the characteristics of entrainment, seems to us to be sufficient evidence for the existence of circannual clocks. Some of our conclusions are based on similarities in behaviour between circannual and circadian clocks. We are aware of the limitations that are implicit in such a formalistic approach, but we are also confident that the march through the 'formal tunnel' (Menaker 1974) is not fruitless. As in circadian rhythm research the analysis of general rhythm properties is of importance for the understanding of many aspects of their adaptive significance. Moreover, a more detailed knowledge of formal properties of circannual rhythms will provide a basis for further physiological studies related to the question whether photoperiod is a proximate cause or a zeitgeber. We are convinced that evolution has not only led to the replacement of ultimate causes by external proximate 'causes' but in many instances by a combination of two proximate factors: an endogenous rhythm and its entraining zeitgebers (Aschoff 1958).

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Avian Orientation and Navigation: New Developments in an Old Mystery

William T. Keeton

My purpose in writing this paper is to provide the reader with some understanding of modern-day ideas and current research thrusts in the very active field of bird orientation and navigation. Although the focus will be on research done in the 1970s, I shall review very briefly older background work on the sun and star compasses before moving on to discuss, first, some newly discovered (or newly re-examined) cues thought to be used by orienting birds, and, second, some approaches presently being pursued in the attempt to learn how the many different cues are integrated by orienting birds. I hope that I shall succeed in communicating the sense of intense excitement that now prevails in this branch of ornithology.

The more familiar orientational cues

One of the earliest and most stimulating discoveries in the field of avian orientation and navigation was that celestial cues – the sun and the stars – play a fundamental role in bird orientation. Thus, more than twenty-five years ago, Gustav Kramer (1952) and his students showed that birds possess what has come to be called a sun compass. And, following up Kramer's (1949, 1951) early observations that several species of nocturnal migrants exhibit oriented migratory restlessness (Zugunruhe) in circular cages under clear night skies, Sauer (1957) found that such nocturnal orientation depended on the stars, thus laying the basis for what is now known as the star compass. Because the sun and star compasses are so important, both in avian orientation itself and in the role they have played in the development of this field of ornithology, we should pause to review quickly how they are thought to function.

The overwhelming preponderance of evidence indicates that solar cues are used by birds only as a simple compass, not as the basis of a bicoordinate navigation system as proposed by Matthews (1953, 1955) in his sun-arc hypothesis (for a summary of the evidence, see Keeton, 1974a). In other words, it appears to be only the sun's azimuth (direction from the observer) that provides the bird with orientational information. But the azimuth can provide such information only if the time is known, so that compensation can be made for the sun's changing position throughout the day, from easterly in the morning to south at noon to westerly in the afternoon (in the northern hemisphere). That birds do indeed couple their internal clock (circadian rhythm) with their observation of the sun's azimuth in determining compass directions was clearly demonstrated by Kramer (1953a) and by Hoffmann (1954), working with caged birds. Later, Schmidt-Koenig (1960) extended this finding to free-flying homing pigeons. He showed that pigeons whose internal clocks had been experimentally shifted 6 hr out of phase with true sun time chose initial bearings roughly 90° from those of control pigeons when released at a distant test site (Fig. 1 A); their clocks had been shifted a quarter of a day, and, as a consequence, they misread the sun compass and chose bearings a quarter of a circle different from those of the controls.

As in the case of the sun, the evidence is overwhelming that the stars provide only compass information for birds, even though they could potentially be used in true

Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA.

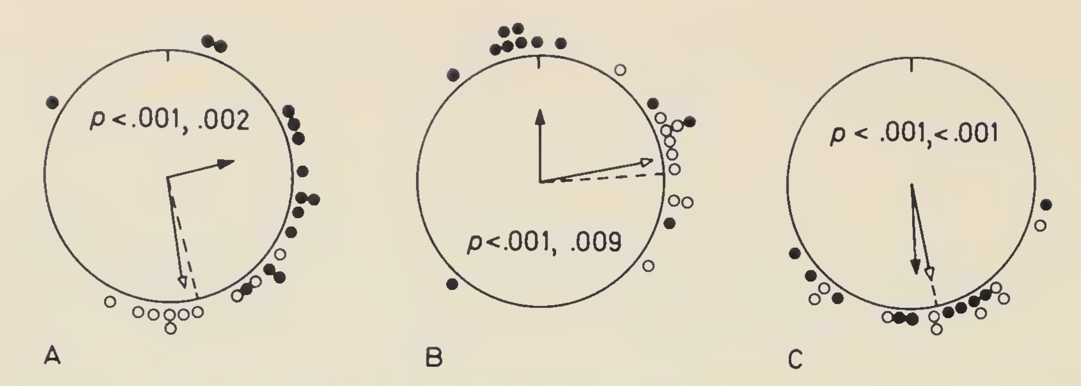


FIGURE 1. Vanishing bearings of pigeons that have been clock-shifted 6 hr fast.

A: Experienced pigeons released on a sunny day at a distant site. The mean bearing of the clock shifted birds is roughly 90° to the left of that of the controls.

B: Experienced pigeons released on a sunny day at a site less than a mile from home, where the landscape should be completely familiar. Again, the mean bearing of the clock-shifted birds is roughly 90° to the left of that of the controls.

C: Experienced pigeons released on a totally overcast day at a distant unfamiliar site. Both the clock-shifted and the control birds are homeward oriented, and there is no indication of a difference between them, which suggests that, in the absence of the sun compass, the pigeons use orientational cues that do not require time compensation.

In this and later figures showing bearings, north is indicated by a small line at the top of the circle, and the home direction by a dashed line reaching the perimeter of the circle. The bearing of each individual bird is shown as a small symbol on the outside of the circle; where two treatments are included on a single circle, the bearings of the controls are shown as open symbols and the bearings of the experimental birds as filled symbols. The mean vectors are shown as arrows (with open or filled heads, respectively), whose length is drawn proportional to the tightness of clumping of the bearings (i.e. the longer the vector – at maximum reaching the perimeter of the circle – the better oriented the sample of bearings). The uniform probability under the RAYLEIGH test is given inside the circle; the first value is for the controls and the second for the experimentals.

bicoordinate navigation (for a thorough discussion, see EMLEN, 1975a). SAUER (1957) thought that the star compass, like the sun compass, required time compensation. But in a detailed study of the migratory orientation of the Indigo Bunting *Passerina cyanea*, EMLEN (1967) found that this species uses star patterns to determine directions, a process that does not require time compensation (Fig. 2). It seems likely that this is true of other species as well (EMLEN, 1975a). Thus the way birds read the star compass differs fundamentally from the way they read the sun compass.

Although the sun compass during the day and the star compass during the night are certainly dominant orientational cues for birds, there is now abundant evidence that neither is essential for proper orientation. Thus experienced homing pigeons can orient accurately homeward from distant unfamiliar release sites under heavy total overcast (Fig. 1 C) (KEETON, 1969, 1974a). And tracking-radar studies have regularly revealed nocturnal migrants in oriented flight under heavy overcast when the stars are not visible (e. g. NISBET & DRURY, 1967; STEIDINGER, 1968; WILLIAMS et al., 1972; GRIFFIN, 1972, 1973). It is apparent, then, that though birds often use celestial cues when they are available, they can use alternative cues when necessary. In short, avian orientation systems include redundant, or back-up, cues (KEETON, 1974a; EMLEN, 1975a).

It is also important to point out, as KRAMER (1953b) did long ago, that other environmental cues must provide goal-orienting birds with an analog of map information.

A compass alone cannot tell a bird where it is nor which direction it should fly to reach its destination.

If celestial cues do not suffice for avian orientation, what other possibilities should be considered? Certainly the most obvious would be familiar landmarks, but, curiously enough, birds seem to make only minimal use of these. Radar studies strongly suggest that landmarks play little role in migratory orientation (Emlen, 1975a; Emlen & Demong, 1978). Pigeons clock-shifted 6 hr out of phase with true sun time and released half a mile from their home loft, in a area they have flown over every day when exercising, usually choose bearings deflected 90° from the homeward course (Fig. 1 B) (Graue, 1963; Keeton, 1974a); the birds act as though they have never before seen the place! Even more remarkable, pigeons wearing frosted-white contact lenses that eliminate image vision beyond two or three meters can orient accurately homeward from distant locations, and can even tell when they have arrived at their goal (Schmidt-Koenig & Schlichte, 1972; Schlichte, 1973).



Figure 2. An example of how north can be located by star patterns. If one draws an arrow running through two particular stars in the cup of the big dipper (Ursa Major), it will point toward Polaris. Although the position of the constellations changes during the night, the same stars always determine an arrow pointing toward Polaris (i.e. toward north, or the pole of the celestial rotations), hence directions can be determined without need of time compensation. Many different star patterns could be used for direction finding in this way.

Another possibility that comes to mind in this age of rocketry is that the birds might have some sort of sophisticated inertial guidance system (Barlow, 1964). Although this possibility cannot be completely ruled out, it seems very unlikely in view of evidence against it from many kinds of investigations, including turn-table experiments (e.g. Griffin, 1940), experiments with deep anesthesia (e.g. Walcott & Schmidt-Koenig, 1973), and experiments with surgical lesions of the vestibular organs (e.g. Wallraff, 1965).

Unusual sensory capabilities of birds

Having eliminated the most obvious cues, we turn next to one of the most active areas of recent orientational research – the investigation of special sensory capabilities of birds (some of them only very recently discovered) that my play a role in the bird's amazing orientational and navigational feats.

Magnetic detection

Although it had often been suggested that birds might be able to derive directional information from the earth's magnetic field, the prevailing opinion of this possibility in the scientific community of the mid 1960s was one of intense skepticism. Reports by Brown

and his colleagues (summarizied in BROWN, 1971) that a variety of invertebrates respond to weak magnetic fields had not been widely accepted, and most investigators thought it very unlikely that any organism could detect a magnetic field as weak as that of the earth (about 0.5 gauss). But beginning in the mid 1960s, and continuing to the present, a group in Frankfurt, led first by F. MERKEL and later by W. WILTSCHKO, intensively investigated the possible role of magnetic cues in avian orientation.

Having first found that European Robins *Erithacus rubecula* exhibit migratorily appropriate orientation in circular test cages when visual cues are unavailable (MERKEL et al., 1964), this group went on to show that the orientation of the Robins could be changed in a predictable way by turning the magnetic field (e.g. making magnetic north in the cage coincide with geographic east), using Helmholtz coils positioned around the test cage (MERKEL & WILTSCHKO, 1965; WILTSCHKO, 1968). Although the technique used by the Frankfurt group was viewed with skepticism by some investigators, and was shown to be very susceptible to artifacts unless great care is taken in conducting the experiments (HOWLAND, 1973), their results were later successfully replicated by WALLRAFF (1972) with Robins, and by EMLEN et al. (1976) with Indigo Buntings.

Following up his earlier work, WILTSCHKO (1972) found that robins accustomed to the normal magnetic field at Frankfurt (0.46 gauss) initially gave random bearings in fields 26% lower (0.35 gauss) or 48% higher (0.68 gauss). However, if the birds were kept in the altered field for a few days, they could then orient in fields as low as 0.16 gauss or as high as 0.81 gauss. A similar sensitivity to altered field strengths was found in Whitethroats *Sylvia communis* and in Garden Warblers *Sylvia borin* (WILTSCHKO & MERKEL, 1971; WILTSCHKO, 1974). It was suggested that the birds' ability to adapt to a range of field strengths would permit them to adjust to the varying magnetic intensities they would encounter at different geographic latitudes during migration.

WILTSCHKO (1972; see also WILTSCHKO & WILTSCHKO, 1972) found, further, that Robins apparently pay no heed to the polarity of the magnetic field, but rather, in the northern hemisphere, take north as that direction in which the magnetic and gravity vectors form the most acute angle (Fig. 3). They are unable to orient in test cages when the magnetic field is entirely horizontal (i.e. has no vertical component), as is the case at the equator. In short, the bird's manner of reading the magnetic compass is very different from our own.

The first good evidence of a magnetic effect on pigeon homing came when KEETON (1971, 1972) found that bar magnets attached to experienced bird's backs often caused disorientation on heavily overcast days, whereas they had little effect on sunny days. WALCOTT & GREEN (1974), using Helmholtz coils on the pigeons' head and neck, exposed the birds to more homogeneous magnetic fields than those produced by KEETON's bar magnets; again there was no dramatic effect on sunny days, but on overcast days the bird's orientation was changed (not merely disrupted) in a manner consistent with WILTSCHKO's formulation of the way the avian magnetic compass works.

Thus emerged the concept that, in the case of homing pigeons, the magnetic field provides compass information that experienced birds use primarily when the sun compass is not available. While this idea is certainly true in some respects, it may also be an oversimplification, because there is a growing body of evidence that magnetic perturbations alter in a small but consistent way the orientation of pigeons on sunny days

(KEETON, 1971; KEETON et al., 1974; LARKIN & KEETON, 1976; WALCOTT, 1977). Moreover, there is also some indication that magnetic information obtained during the outward journey to the release site may sometimes influence the initial orientation of pigeons (R. WILTSCHKO et al., 1978; KIEPENHEUER, 1978; PAPI et al., 1978).

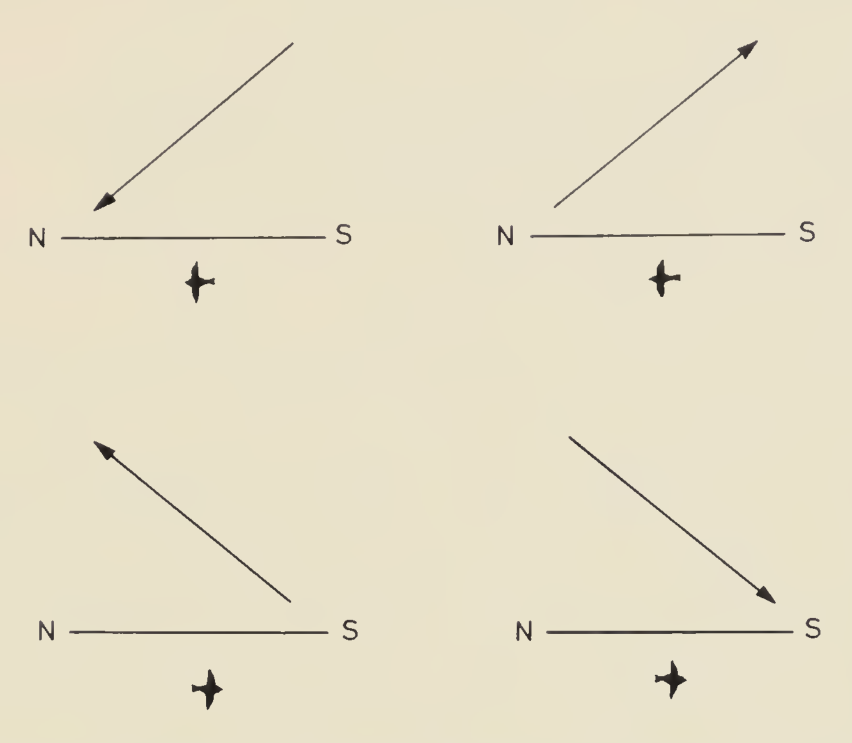


FIGURE 3. The magnetic compass of the European Robin. Top: The birds orient northward in spring, whether the magnetic field vector points north and down (which is the normal condition) or south and up. Bottom: The same birds change their orientation to southward if the magnetic vector points north and up or south and down. In short, it appears to be the alignment of the magnetic vector, not its polarity, that determines the birds' behaviour.

LINDAUER & MARTIN (1968; see also MARTIN & LINDAUER, 1977) have reported convincing evidence that the dance of scout honeybees is influenced by even minor natural fluctuations in the earth's magnetic field. Their results suggest the bees are sensitive to magnetic changes of less than 10^{-3} gauss and very probably of less than 10^{-5} gauss. There is now evidence from several sources that birds are probably equally sensitive. Thus SOUTHERN (1972) has reported for gull chicks, KEETON et al. (1974; see also LARKIN & KEETON, 1977) for homing pigeons, and MOORE (1977) for free-flying migrants that orientation is influenced by natural magnetic disturbances, due largely to events on the sun, such as solar flares. Also indicating a very great magnetic sensitivity is evidence reported by WAGNER (1976) and by WALCOTT (1978) that geographic magnetic anomalies disturb the initial orientation of pigeons. LARKIN & SUTHERLAND (1977) have found evidence that free-flying migrants are influenced by the very weak low-frequency alternating fields produced by the Wisconsin test antenna for the U.S. Navy's proposed Project Seafarer.

In view of the abundant evidence that birds are very sensitive to magnetic stimuli, at least when they are orienting, one would hope that we will soon learn the mechanism of their magnetic sense. Several hypotheses (e.g. COPE, 1973; LEASK, 1977, 1978) have been put forward, but remain inadequately evaluated. Indeed, until very recently no one had been successful in training birds to magnetic stimuli in the laboratory (as opposed to recording

spontaneous reponses), despite numerous attempts (e.g. EMLEN, 1970a; KREITHEN & KEETON, 1974c; BEAUGRAND, 1976, 1977). Finally, BOOKMAN (1977) has reported success training pigeons in a two-choice test where different magnetic conditions provide the information on which the choice must be based. BOOKMAN's procedure differs in at least two obvious ways from previous conditioning attempts, namely the birds are permitted more time to make the choice and they can fly within the test field. BOOKMAN's data suggest that flying (especially hovering) is very important, thought it is not yet known whether the flight is necessary for operation of the detection mechanism per se or whether it merely makes the birds more attentive to magnetic stimuli.

Possible detection of gravity variations

Several years ago, LARKIN and KEETON noticed that often when animals had shown clear responsiveness to magnetic stimuli they had been simultaneously responding to gravity (e.g. LINDAUER & MARTIN, 1968; WEHNER & LABHART, 1970; WILTSCHKO & WILTSCHKO, 1972). Consequently, these investigators sought to determine whether gravity cues might play some role in pigeon homing, especially in situations where the birds are using magnetic information. Being unable to alter gravity in the laboratory, they looked instead for a possible influence of the natural monthly gravitational cycle caused by the changing relative positions of the earth, sun and moon. In six separate test series, conducted during four different years at three different locations, they found a significant correlation between the pigeons' mean vanishing bearings and the day of the lunar synodic month (LARKIN & KEETON, 1978). Suggestive as these results may be, however, they do not prove a direct effect of gravitational changes on the birds' orientation, because some other environmental variables to which birds might be responsive may also be related to the lunar cycle.

Despite the still uncertain meaning of the synodic lunar rhythm found by LARKIN & KEETON, let us consider the possibilities for birds if they could detect minute variations in gravity. Gravity varies not only temporally but also geographically, in both a regular and an irregular manner. The regular variation is in a north-south gradient and is due to the fact that the earth is not a perfect sphere. The irregular variation is due to the differing densities of the material in the earth's crust at different localities. Gravity cues could, then, potentially be useful in navigation, both because they would indicate the north-south axis and because they could provide an additional topography over and above the topographies we normally consider.

If a bird could use the north-south gravitational gradient to determine true (i.e. rotational) north, then magnetic declination (the deviation of magnetic north from true north) might be readable. It happens that declination is one of the very few environmental parameters that vary as a rough analog of longitude, hence its potential usefulness would be very great indeed. Moreover, preliminary results of LARKIN & KEETON (unpublished) suggest that declination may actually be the parameter of the magnetic field that most influences pigeon orientation during magnetic disturbances. Clearly this is a subject worthy of further intensive exploration. It is important to emphasize, however, that there is as yet no direct evidence that birds can detect such incredibly tiny differences in gravity (less than 10 gals) as would be necessary to permit use of gravitational cues in long-distance navigation.

Barometric pressure detection

For birds, which spend much of their time in the air, a sensitive ability to detect changes in barometric pressure would potentially be useful in a variety of ways. Hence it is not surprising that pigeons have recently been shown to possess just such a detection capability (Kreithen & Keeton, 1974a). Other species of birds have not yet been tested for this ability.

One obvious way a bird could use a barometric pressure sense is as an altimeter. The sensitivity found in homing pigeons is sufficiently great so that they should surely be able to detect a change in altitude of 10 m, and indeed it seems likely they may be able to detect a change of as little as 3 m. Not only would an altimeter sense be useful when flying in cloud, but we note also that, if birds really possess the ability to detect changes in gravity, as speculated above, an altimeter would be essential because compensation for altitude would be necessary in view of the fall in gravity with increasing elevation.

Another way birds might use their barometric sense would be in predicting weather changes. A human meteorologist finds a senstive barometer very helpful in such predicting; why should not a bird use its built-in barometer in the same way? There is, of course, a long history of ordinary bird watchers reporting that the birds in their yard seem to show by behavior changes that a weather front is approaching, long before the human observer sees any indication of the front. And, more authoritative, there is convincing recent evidence that birds about to initiate migratory flight are very good meteorologists indeed (Emlen, 1974a). Thus, in eastern North America, major autumnal movements tend to occur on the east side of a high-pressure cell following passage of a cold front, and major spring flights tend to cencentrate on the west side of a high pressure area ahead of an advancing low-pressure cell (Richardson, 1971, 1972). Many migrants, especially small song birds, seem to be quite accurate at predicting early in the evening, when they are still on the ground, what the wind conditions aloft will be later that night; they go up in greatest numbers when the winds aloft will be favorable.

Finally, the last few years have witnessed a growing interest in the possibility that weather factors may not only be important in determining the intensity of migratory movements, or in influencing the bioenergetic cost of migration, but also in providing useful orientation cues (Griffin, 1969; Emlen, 1975a). Wind directions, pressure patterns in the atmosphere, and patterns of air turbulence are among the meteorological factors that could potentially provide orientational information, and the detection of these would surely be facilitated by the bird's barometric sense. In some situations (but certainly not all), however, passerines may not get directional information per se from the winds, but simply fly downwind once aloft (Gauthreaux & Able, 1970; Able, 1973, 1974a; Williams & Williams, 1978; for contrary evidence, see Able, 1974b).

Infrasound Detection

Although the literature would lead one to think the lower frequency limit of bird hearing would be about 100 Hz, Yodlowski et al. (1977) have recently announced the startling discovery that homing pigeons are sensitive to frequencies lower than 1 Hz. Indeed, the audiogram for the pigeon worked out by Kreithen & Quine (in press) shows sensitivity down at least to 0.05 Hz (Fig. 4). Admittedly the very low frequency sounds

must be very loud to be detected, but natural environmental sounds are often that loud. We humans, being deaf to such low frequencies, tend to forget that the environment is very noisy in the low-frequency range. The pigeons' sensitivity is, in fact, at the level it should be if meaningful signals are to be extracted from the noise. What is important is not absolute sensitivity but environmentally relative sensitivity.

Detection of infrasound by birds raises an intriguing new orientational possibility. Because attenuation is proportional to the square of frequency, infrasonic frequencies as low as those the birds can detect may travel hundreds or even thousands of miles with little energy loss. Potentially, then, pigeons might be able to minitor distant infrasonic sources, such as mountains whistling because of winds blowing across them, and to use these as a rough system of beacons for determining position.

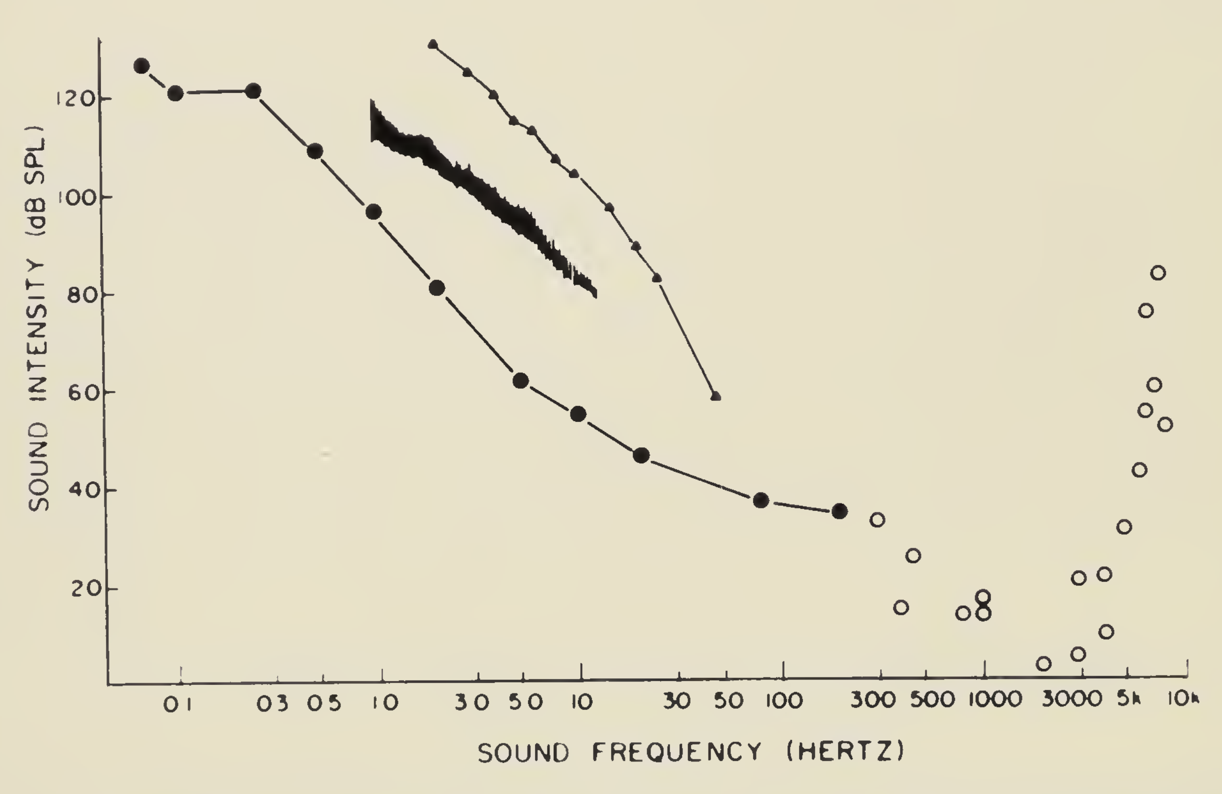


FIGURE 4. A behavioural audiogram for the homing pigeon. Open symbols (in the standard acoustical range) represent data from the older literature. Black circles indicate newly determined intensity thresholds (dB SPL) in the lower-frequency range. The series of vertical bars illustrate the approximate intensity of natural environmental infrasounds. The pigeons' sensitivity is sufficient so that these natural infrasounds should be audible. By contrast, the low-frequency sensitivity of human beings (black triangles) is not sufficient to permit hearing of the natural infrasounds.

But if pigeons are to use infrasounds in this way, they should be able to tell from what directions the sounds come, yet binaural comparisons would be impossible for such very long wavelengths (over 3 km at 0.1 Hz). A possible way around this problem comes from the work of QUINE (in prep.), who finds that pigeons' frequency discrimination in the infrasonic range is sufficiently good so that doppler shifts in apparent frequency induced when a bird flies toward and then away from an infrasound source would be well within the bird's ability to detect. Thus pigeons may be able to get directional information from infrasounds while in flight, even if they cannot do so while perching. Field experiments to evaluate this possibility are now in progress at Cornell.

Polarized light detection

The discovery by Kreithen & Keeton (1974b) and by Delius et al. (1976) that homing pigeons can detect the polarization of light may mean that these birds, like honeybees, can continue using a derivative of the sun compass on partially overcast days, when the sun's disk is hidden from view but some blue sky remains. This is possible because of the geometric relationships between the position of the observer, the plane of polarization of sunlight, and the position of the sun, which permits derivation of the sun's position if the polarization can be detected. Actual use of polarized light by orienting birds in the field has, however, not yet been studied.

Ultraviolet light detection

Yet another addition to our knowledge of avian vision is the recent discovery by Kreithen & Eisner (1978) that homing pigeons can see ultraviolet light (see also Delius & Emmerton, 1978). This raises the question, now under investigation at Cornell, whether the pigeons perform their analysis of polarization in the ultraviolet wavelengths, as honeybees do.

Olfaction

Olfaction, unlike most of the other sensory capacities discussed above, is not a recently discovered sense. But the possibility that it may play an important role in avian navigation is new. It was in 1972 that Papi et al. first put forward their olfactory navigation hypothesis. Briefly, they propose that young pigeons at the home loft would learn to associate particular odors with winds fron certain directions. Thus odor A might arrive at the loft primarily on winds from the north, odor B on winds from the east, etc. A bird released at a distant site, say north of home, would detect a strong odor of A and therefore determine its position to be north of home. The bird would then use one of its compass systems to locate south, and begin its homeward flight.

Papi and his colleagues have performed a long series of ingenious experiments to test their hypothesis, and have reported consistently positive results (for summary, see Papi, 1976). These experiments have included painting strongly odorous substances (e.g. α-pinene) on the birds' noses just before release, transporting birds to release sites along strongly divergent routes or under altered olfactory conditions, unilateral and bilateral sectioning of the olfactory nerves, and exposing young pigeons to altered olfactory experiences at the home loft. Unfortunately, attempts to repeat some of these experiments at Cornell yielded generally negative results as far as orientation was concerned, though there was sometimes an effect on homing success (Keeton, 1974b; Keeton & Brown, 1976; Keeton et al., 1977). Similar attempts at Tübingen yielded either negative (Schmidt-Koenig & Philips, 1978) or ambiguous (Hartwick et al., 1978) results.

In an effort to resolve the differences between the Pisa and Cornell groups, six series of collaborative experiments were performed at Cornell in 1977. The overall result of these experiments was that, with the exception of deflector-loft experiments, to be discussed later, we found no consistent effect of olfactory interference or deprivation on initial orientation, but we did often find an effect on homing success from distant unfamiliar release sites (Papi et al., in press). Unfortunately these results are interpreted one way by

the Cornell investigators and another way by the Italian investigators, hence the question of the role of olfaction in avian orientation remains unresolved. Readers should be forewarned that the remainder of the present discussion of olfaction is a biased one, since I am a major party to the disagreement.

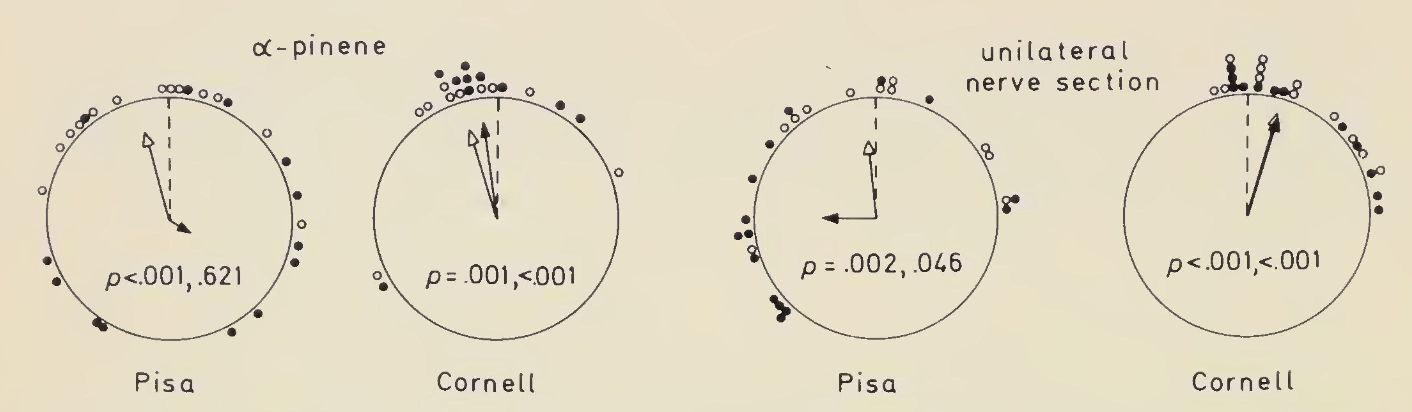


FIGURE 5. A comparison of results from Pisa and Cornell in two tests of the olfactory-navigation hypothesis. Left: At Pisa, pigeons with α-pinene painted on their nostrils (black symbols) were disoriented whereas control pigeons (open symbols) were homeward oriented. By contrast both control and experimental bird were oriented at Cornell. Right: In releases of pigeons with unilateral olfactory-nerve sections, the experimental birds (contralateral nostril plugged) oriented differently from the controls (ipsilateral nostril plugged) at Pisa but not at Cornell. The home bearing has been set at O° in all four cases, to facilitate comparisons.

Let us look more closely at the collaborative results concerning initial orientation. (1) We found no effect on orientation of painting α-pinene on the birds' noses, whereas BENVENUTI et al. (in press) have found a clear disorienting effect in Italy (Fig. 5). (2) Inserting plastic tubes in the birds' nostrils to eliminate olfaction had little effect on orientation, whereas HARTWICK et al. (1977) have reported an effect in Italy. (3) Pigeons subjected to unilateral section of the olfactory nerve and then released wearing a plug in the contralateral nostril (controls wore a plug in the ipsilateral nostril) showed no marked orientational deficit, whereas BALDACCINI et al. (1975) did find an orientational effect of such treatment in Italy (Fig. 5). (4) We found an effect on orientation of only one out of three outward-journey detours (three detours tried earlier by KEETON, 1974b also showed no effect), whereas PAPI et al. (1973) report a consistent effect of such detours in Italy. I conclude, then, that there must be major differences in the homing behavior of the Italian and Cornell pigeons, and that it will be a fascinating topic for future research to determine why Italian pigeons seem to rely so much more heavily on olfaction than Cornell pigeons do. (This is not, however, the first example of major geographic differences in avian orientation, for nocturnal passerine migrants in the southeastern United States nearly always fly downwind, whereas the same species in the northeastern part of the country only rarely do so if the wind direction is inappropriate [see ABLE, 1978].)

In one series of collaborative experiments, we were successful in repeating the Italian group's results on initial orientation. This series utilized the deflector-loft technique so imaginatively designed by BALDACCINI et al. (1975b). In these experiments, pigeons were exposed in their home lofts to winds – and the odors they are presumed to carry – deflected either clockwise or counterclockwise (Fig. 6). When tested at release sites, the pigeons chose bearings to the right or left of control pigeons, as predicted by the olfactory

hypothesis (Waldvogel et al., in press). These results may well indicate that olfactory cues are sometimes used by the Cornell pigeons, though no final decision can be made until experiments that control for the various other orientationally relevant factors altered by the deflectors are performed.

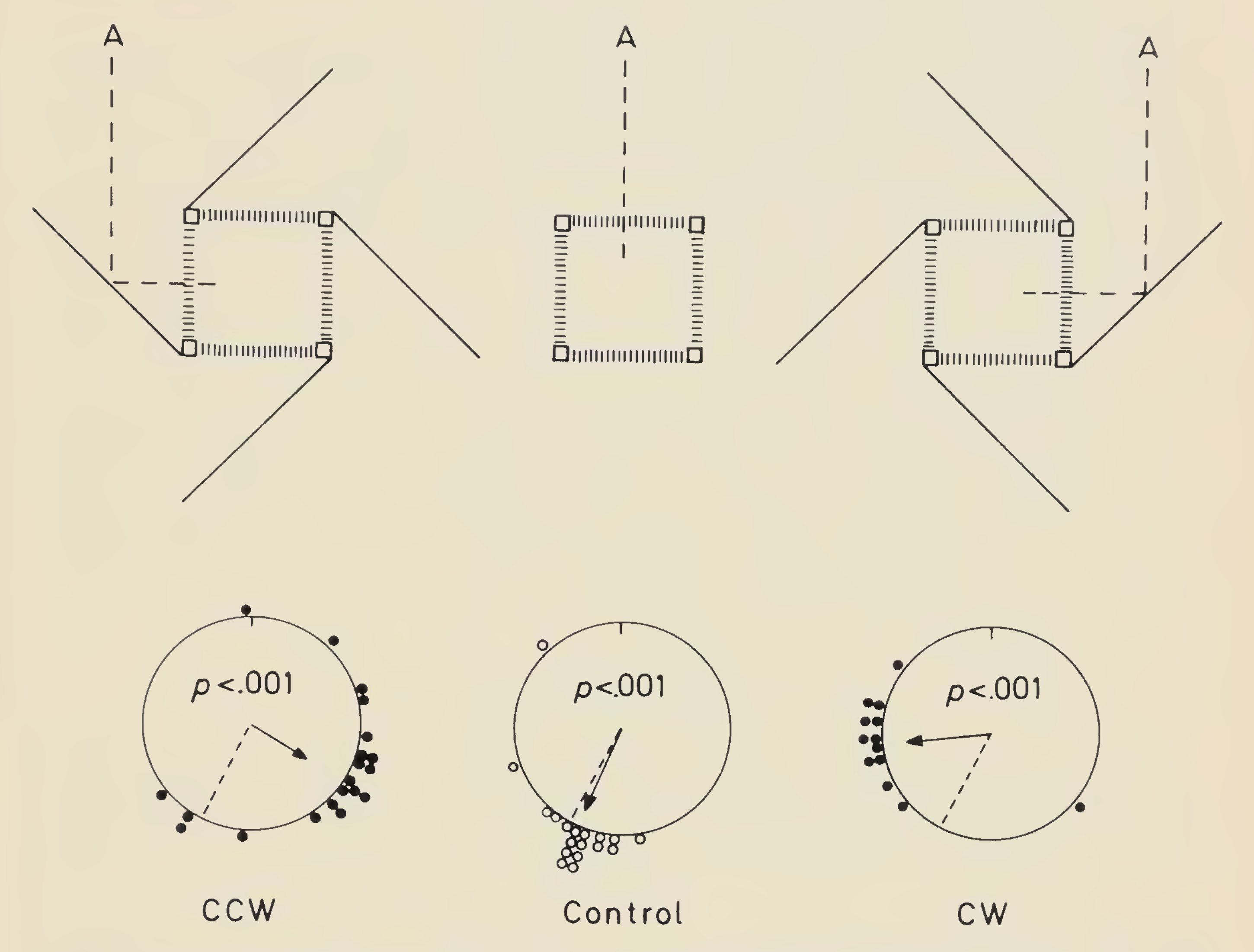


Figure 6. The deflector loft experiments. Top: All three lofts (control loft in center, lofts with deflectors on each side) have walls that allow free flow of air. Winds from the north, presumably carrying odour A, enter the control loft from the north, but they enter the other lofts from the east and west because of the deflectors. Bottom: Bearings of pigeons released north of home. The control birds, which had earlier experienced normal air flow (i.e. A winds from the north) oriented properly southward, toward home. By contrast, the CW birds, which had experienced A winds from the east, oriented more westerly, and the CCW birds, which had experienced A winds from the west, oriented easterly. (Redrawn from Baldaccini et al., 1975b).

There is no question that techniques such as olfactory nerve section or insertion of plastic tubes into the nostrils do usually result in much poorer homing success from distant unfamiliar release sites. As in Italy, this had been found at Cornell (Keeton et al., 1977; Hermayer & Keeton, in prep.) and was confirmed by the collaborative experiments. It is in interpreting this effect on homing that the Italian and Cornell groups differ the most. Papi and his colleagues feel the poor homing means that olfactory cues play an irreplaceable role in homing from unfamiliar sites – that birds are unable to home from unfamiliar sites when deprived of olfactory information. My colleagues and I feel, on the other hand, that since the olfactorily deprived birds usually depart from the release site on

a proper course, their poorer homing may have nothing to do with navigation but may merely indicate a diminished motivation that results in the birds' landing when only part way home. We are concerned about the motivational effects of surgical or other procedures that produce trauma, especially when the trauma is to a part of the respiratory system, on which flying birds must make very heavy demands.

We attempted to evaluate our suggestion by airplane-tracking pigeons in one of the collaborative experiments with nasal tubes. Unfortunately, our suggestion proved almost too true – all five of the experimental birds that were tracked soon landed and we were unable to get as much detail about the flight course as we had hoped. However, before they landed, these birds were flying roughly the same course followed by control birds. Hence, in my opinion, there was no indication of disorientation but rather abundant indication of diminished motivation.

In summary, my appraisal of the role of olfaction in avian navigation is that it is very likely that odors constitute one of the many sources of information birds may use in navigating. Olfactory cues appear to be used more by Italian than by Cornell pigeons, for reasons yet to be determined. But I doubt that olfaction will be found to play as essential a role in avian navigation as Papi and his colleagues have proposed. Indeed, I am not convinced that any single cue so far discovered is essential; there seems to be so much redundancy in the avian navigation system that experienced birds can orient when only a few from the full panoply of cues are available.

The Integration of orientational cues

From all that has been said above, it should be clear to the reader that birds can use many different orientational cues, some of them redundant. These cues can be integrated in a variety of ways – according to different weighting schemes, if you will – depending on the birds' age, experience, and species, and on weather conditions and the season of the year. The old hope that one simple system would be found to explain all of avian orientation has gone aglimmering. Hence one of the chief thrusts of current orientational research is the attempt to learn how the different cues are integrated and what constraints there are on the amazing flexibility of avian navigation systems.

Studies of integration: the ontogeny of orientational behavior

One powerful way of teasing apart the many elements of avian orientation systems is to manipulate the early development of those systems. By so doing, one can often get young birds to omit one or more of the usual cues or to adopt an atypical weighting scheme so that cues that would normally be secondary or tertiary become primary and thus easier to study.

In a series of experiments on the ontogeny of stellar orientation in Indigo Buntings, EMLEN (1972) found that there is a critical period during which young buntings learn to read the star compass. If the buntings have had a view of the starry sky during the weeks preceding the start of their first autumnal migration season, they can orient properly when that season begins. But if they have not seen the night sky until after the first migration season has begun, they never learn to use the star compass, no matter how often they see the sky thereafter.

Emlen (1972, 1975b) also showed that young buntings respond initially to the apparent rotation of the starry sky during the night. The axis of this rotation is north-south, hence it can provide compass information. But detecting the rotation probably takes considerable time – the rotation could not be determined at a glance. It is understandable, therefore, that the birds do not long depend on the axis of rotation per se; rather they soon learn star patterns that will indicate where the axis is, and thereafter they rely exclusively on those patterns. In other words, the axis of rotation functions in ontogeny only as the reference against which the star compass is initially calibrated. Thus, when Emlen exposed hand-reared young buntings to a planetarium sky rotating around an incorrect axis – one for which Betelgeuse was the pole star – the buntings learned to use the stars in the circum-Betelgeuse portion of the sky and, consequently, they oriented in an inappropriate direction when later tested under a normal sky. When retested a year later, after extensive exposure to the normal sky, they had not corrected their orientation; what they had learned during the critical period in their early life still dominated their behavior.

In orientation studies with young first-flight pigeons (i. e. very young birds released for their first homing flight), Keeton & Gobert (1970) found that these birds appear to require the sun compass for orientation; if they are released under heavy total overcast they usually depart randomly, even though experienced pigeons can orient under such conditions (Keeton, 1969). Moreover, first-flight youngsters appear to require magnetic cues also; they usually depart randomly, even on sunny days, when wearing bar magnets attached to their backs (Fig. 7) (Keeton, 1971). In short, the first-flight birds need both sun and magnetic cues, whereas experienced pigeons need only one or the other. It seems, then, that these young inexperienced pigeons are integrating cues in a manner quite different from that used by experienced birds. Perhaps the effect of experience is merely to enable them to get by with less information, but alternatively, the experience may help them establish a hierarchy of choice, so that they can later deal with situations in which two or more cues give conflicting information.

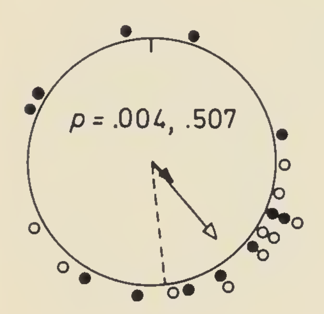


Figure 7. The orientation under a spring planetarium sky of Indigo Buntings in spring and "autumnal" physiological conditions. The birds in spring oriented north-northeastward, the usual direction for this species. The birds brought artificially into autumnal condition oriented south-southeastward. (Redrawn from data in Emlen, 1975a.)

In some cases, the effects of experience and of increasing age may be essentially interchangeable. For example, in a lengthy study of the effects of clock-shifts on the orientation of first-flight pigeons, Keeton & Brown (in prep.) found that very young first-flight birds (less than 10 weeks old) seldom respond to 6 hr clock-shifts by choosing bearings deflected 90° from those of control birds; instead, they either orient similarly to the controls or depart randomly. But if they have had previous homing flights – or even if they have simply "trained themselves" by ranging (i.e. by flying away from the vicinity of the home loft during their daily exercise flights) – then even birds as young as 7 weeks old respond to clock-shifts like experienced adults. Birds that have neither ranged nor had previous homing flights but that are more than 18 weeks old also respond to clock-shifts

like experienced adults. In other words, either homing experience or increasing age can cause maturation of orientational responsiveness to clock-shifts.

As an example of an experimental manipulation that results in young birds' omitting a normal cue, we can cite the studies of WILTSCHKO, WILTSCHKO, BROWN & KEETON (in prep.) with so-called no-sun pigeons. These investigators found that young pigeons raised without ever having a chance to see the sun (they were flown for exercise only on overcast days) could orient perfectly well when released under total overcast for their first homing flight, even though normal first-flight pigeons vanish randomly under total overcast (KEETON & GOBERT, 1970). Having never viewed the sun, the no-sun pigeons had not incorporated it into their navigation system and hence had no difficulty orienting when it was missing.

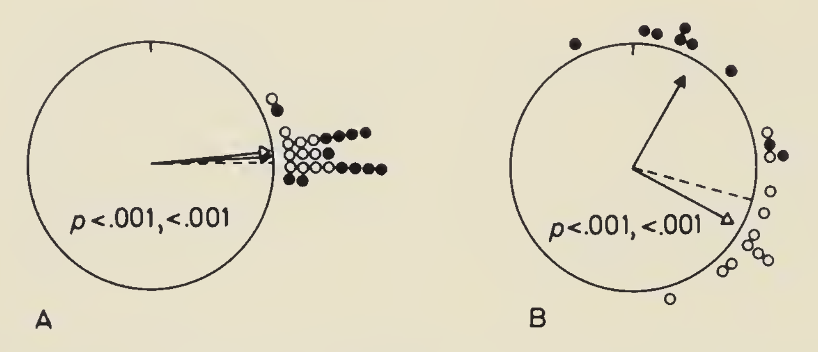


FIGURE 8. Bearings on a sunny day of first-flight pigeons wearing magnet bars or brass bars. The magnet-laden pigeons (black symbols) vanished randomly, whereas the brass-laden birds (open symbols) were well oriented.

Studies of the ontogeny of the sun compass in pigeons have revealed that the coupling of times, directions, and sun azimuths is not inherited but must be learned (WILTSCHKO et al., 1976). Thus young pigeons reaised under a permanently 6-hr-slow clock-shifted photoperiod orient normally, with no indication of the deflection seen in ordinary clocks-shifts (Fig. 8 A). The birds appear to have learned that the "morning" sun is in the south, the "noon" sun is in the west, etc. When these birds are moved to a normal photoperiod and retested after five or six days, they then show bearings deflected 90° from the controls (Fig. 8 B); being put in a normal photoperiod has the same effect on them as a 6-hr-fast clock-shift has on normal pigeons. These results indicate that the sun compass must be calibrated, which suggests that it may be a derivative compass – that there may be some other more fundamental directional cue that functions as the reference for calibration. One current line of research is the attempt to determine what that reference cue might be.

Studies of integration: manipulation of physiological condition

EMLEN (1969) has pursued the question whether it is the seasonal differences in the temporal positions of the stars that determines southward orientation by migratory birds in autumn and northward orientation in spring, or whether the differences in orientation result from corresponding differences in the physiological condition of the birds. By manipulating photoperiods, he contrived to bring one group of male Indigo Buntings into autumnal condition at the same time that another group was in spring condition. He then tested both groups simultaneously under a spring sky in a planetarium. The birds in autumnal condition oriented southward, whereas the birds in spring condition oriented

northward (Fig. 9). Since the two groups saw indentical star patterns, Emlen concluded that their different directions of orientation were due to their physiological conditions, not to the environmental stimuli. He predicted that the important factor would be found to be hormonal.

Later studies by Martin & Meier (1973) supported Emlen's prediction by showing that the orientation of White-throated Sparrows *Zonotrichia albicollis* in circular cages can be reversed by altering the temporal pattern of administration of prolactin and corticosterone. Thus, birds given injections of prolactin 4 hr after injections of corticosterone orient southward, whereas birds given the prolactin 12 hr after corticosterone orient northward.

Further studies utilizing hormonal manipulations promise to provide new insights into the seasonal changes in the cue-integration systems used by the birds.

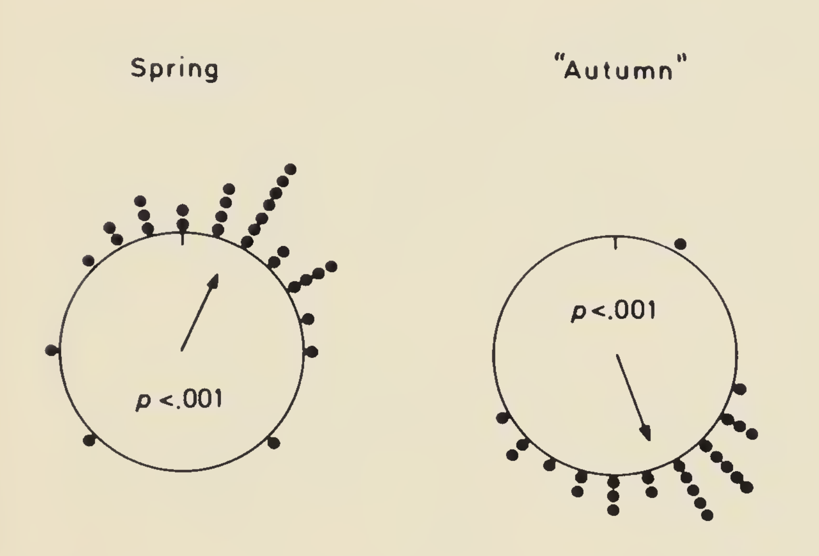


Figure 9. Bearings of pigeons subjected to a "permanent" 6 hr slow clock-shift.
Left: While still living under the shifted photoperiod, the experimental birds orient like the controls, toward home.
Right: When retested 5 days after being moved to the normal photoperiod, the experimental birds choose bearings deflected clockwise from those of the controls.
(From Wiltschko et al., 1976.)

Studies of integration: conflicts between cues

Another method for getting at the question of the relationships between cues is to pit one cue against another in orientational experiments. Let us examine a few recent examples of investigations using this approach.

Wiltschko & Wiltschko (1975) have conducted circular-cage experiments in which migratory birds are able to see the starry sky while experiencing a magnetic field that has been turned by Helmholtz coils. In other words, the birds receive conflicting information from the star and magnetic compasses. The Wiltschkos report evidence that their birds (both robins and warblers) periodically use the magnetic field to recalibrate their star compass. The birds may then orient by the stars for a day or so before again taking a magnetic reading. The process is similar to one a person might use if, after consulting his magnetic compass, he then walked toward a distant tree seen to be in the desired direction; the person might not take another magnetic bearing until he needed to recheck the visual marker or to choose a new one. Wiltschko & Wiltschko (1976) also report that the birds can use the magnetic field to calibrate an entirely artificial "star" pattern.

It is important to note the difference between these results of the Wiltschkos, in which magnetic cues appear to be used to calibrate the star compass, and the results of Emlen (1970b, 1972), in which the axis of celestial rotation is used. It is possible that the differences are due to the different species used in the two studies. It seems more likely,

however, that the main difference is that Emlen was studying the original calibration of the compass by premigratory young birds, whereas the WILTSCHKOS were testing recalibration by actively migrating birds. Nonetheless, it remains unclear why Emlen's buntings, which have often been tested in a planetarium with the celestial axis not aligned along magnetic north-south, have shown no indication of recalibrating their star compass. Further work is needed on this topic.

Several series of experiments have been conducted at Cornell in which homing pigeons being clock-shifted 6 hr are permitted exposure to the sun and other natural cues during the shifting process. Pigeons allowed to sit in a wire aviary during the overlap period between their shifted day and the real day gave no indication that they derived any orientationally meaningful information from the sun except that the light was on; the timing information potentially available in the sun's position on its arc appeared to be ignored (ALEXANDER & KEETON, 1974).

Extending this approach a step farther, KEETON & ALEXANDER (in prep.) tried letting pigeons in the process of being clock-shifted fly for exercise during the overlap period between the shifted and real days. Now there was an effect on orientation. Such birds, when tested at a distant release site, usually (but not always) chose initial bearings deflected less than the expected 90° from those of the control birds (the effect differed somewhat depending on the birds' ages). Apparently flight, as opposed to merely sitting in an aviary, had made the birds more responsive to the conflict between their sun compass, their magnetic compass, their visual contact with the loft, and other relevant cues, with the result that the birds given exercise flights during shifting had altered the way they integrated the various cues. EDRICH & KEETON (1978), investigating how much flight is required to produce this effect, found that even pigeons exercised only in 7.3 m long flight cages later chose bearings deflected less than those of normally clock-shifted birds. Further experiments are needed to clarify what cues the clock-shifted birds are using to correct for the erroneous information they get from the sun compass.

Studies of integration: radar tracking of known individuals

In the past, most radar studies of bird migration have used surveillance radar to monitor migratory movements. While this approach has yielded invaluable information concerning flight paths and concerning the relationships between migratory intensity and accuracy and the weather, it has not been suited to study of the orientation of known individual birds. However, EMLEN & DEMONG (1978) have recently used a large tracking radar at the Wallops Island, Virginia, NASA base to follow individual White-throated Sparrows previously captured and assayed for stage of molt, amount of fat, and intensity of Zugunruhe. The sparrows could be released aloft under various weather conditions (including ones when the birds would not normally begin a migratory flight) and after they had been subjected to various manipulations, such as clock-shifting or having a magnet attached. It was thus possible for Emlen and Demong to investigate the decision-making stage of free-flying migration under conditions when different weightings of orientational cues might be expected.

Amongst their many results, EMLEN & DEMONG (1978, and in press) found that information from viewing the setting sun probably plays an important integrative role during the transition between daylight and darkness. Under overcast skies at night, birds

that had not seen sunset oriented poorly whereas those that had seen sunset oriented well. This discovery raises a host of new questions for further investigation. For example, might sunset function as a reference for calibration of other cues? And if so, which cues?

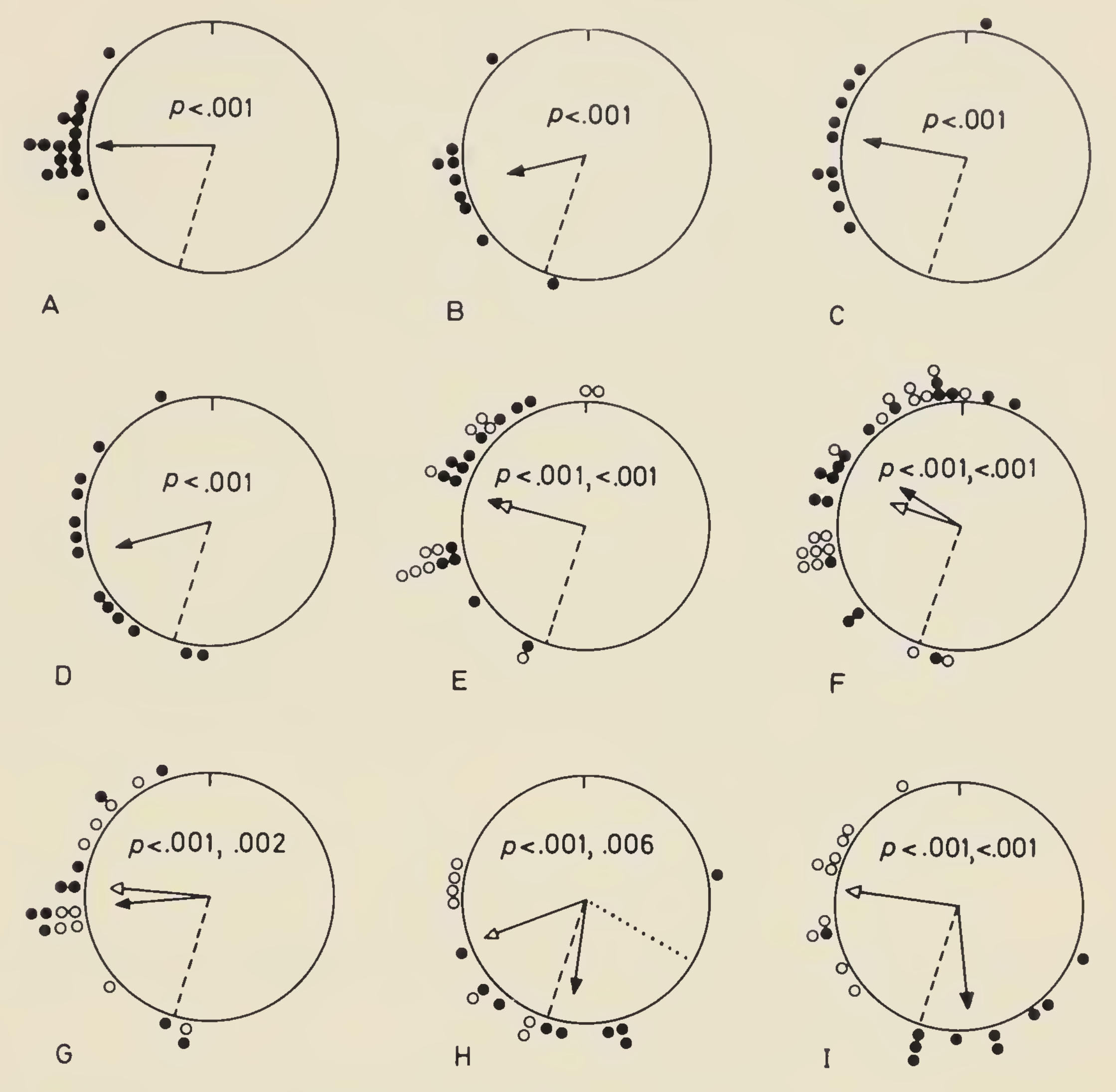


Figure 10. Bearings of Cornell pigeons released at Castor Hill Fire Tower (143 km NNE of the loft).
A: Experienced birds new-to-site customarily depart in a direction 60° to 80° clockwise (westerly) from home.
B: Birds with prior releases from this site usually continue to choose bearings markedly westerly from the home direction.
C: First-flight youngsters also choose westerly bearings.
D: Even under total overcast, experienced birds new-to-site depart in a westerly direction.
E: The bearings of experienced birds new-to-site are nearly identical, whether the birds are wearing magnet bars (black symbols) or brass bars (open symbols).
F: Experienced birds new-to-site choose westerly bearings, whether they are wearing frosted-white contact lenses (black symbols) or clear lenses (open symbols).
G: The bearings of experienced birds new-to-site whose beaks and noses had been painted with α-pinene in vasoline (black symbols) did not differ significantly from those of control birds treated with plain vasoline (open symbols).
H: The bearings to pigeons brought from Schenectady, New York (black symbols), were deflected clockwise from their home direction (dotted line) in a manner similar to the deflection of the bearings of Cornell birds (open symbols) from the direction to Ithaca (dashed line); it therefore appears that some cue basic to pigeon navigation is rotated clockwise at Castor Hill, and that pigeons with different destinations read the cue in the same manner.
I: Although pigeons clock-shifted 6 hr fast choose bearings (black symbols) that are more nearly homeward oriented than those of normal pigeons (open symbols), their homing success is considerably poorer.

Studies of integration: release-site biases

Many investigators have noticed that each release site used for homing pigeons can be characterized by a preferred departure direction that often deviates somewhat from the true home direction; this release-site bias may be only a few degrees to the left or right of home, or at some locations it may be as much as 60–80 degrees (KEETON, 1973). Curiously, the bias is usually not much affected by the previous experience of the birds (Fig. 10 A, B, C). It remains on overcast days (Fig. 10 D) and when the pigeons are wearing magnets (Fig. 10 E), hence the bias is probably not a function of either the sun or magnetic compasses. Tests with frosted contact lenses indicate the bias is not due to the birds' visual perception of the surrounding landscape (Fig. 10 F). The preferred direction is not altered by application of α-pinene to the birds' noses (Fig. 10 G), hence it seems unlikely that the bias has anything to do with olfactory position-determination in the manner proposed by PAPI et al. (1972). Pigeons from other lofts often choose bearings at these sites that are comparably deflected from their own home directions (Fig. 10 H). Bank Swallows *Riparia riparia* show similar biases at these sites, so the biasing factor (or factors), whatever it may be, is apparently not unique to pigeons (KEETON, 1973).

The hope has been that studies of release-site biases would help reveal local factors that might be at least a part of the long-sought navigational map, and how those factors are integrated with the orientational cues already known. So far, unfortunately, that hope has not been realized. All efforts to explain the biases have failed. Nonetheless, this approach seems worth continued effort.

Concluding comments

From the above account, it should be apparent to the reader that avian orientation and navigation is one of the most active fields of ornithological research today. Our whole way of thinking about the subject has changed radically in less than a decade, and the change continues unslowed. A host of new cues are being discovered, and a variety of ways of examing the integration of cues are being pursued. New information is being learned so fast that it is difficult for those outside this field to keep up with it. Yet, despite all the exciting new information and all the impressive progress that has been made, we still cannot put together all the known elements to construct orientational and navigational systems that can do what the birds themselves can do. Clearly, there is much more to be learned. The search for the solution to the mystery of avian orientation and navigation must go on.

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Survival of young Great Tits, *Parus major*

C. M. Perrins

Introduction

Shortly after he became Director of the Edward Grey Institute, Dr. David Lack visited Dr. H. N. Kluyver in Holland. As a result of that visit, David Lack started a population study of the Great Tit *Parus major* at Oxford. The location of this study is Wytham Wood, about 5 km west of the City of Oxford. The wood is owned by the University and is about 240 ha in extent. The study started in 1947 and we have breeding records of the Great Tits and Blue Tits *P. caeruleus* in the woodland ever since that date, this being the 32nd year. Initially, the study concentrated on a small section of the wood, Marley, an area of about 27 ha. During the period 1958–63 I gradually extended the study area until almost all the wood was included. Since about 1965 we have caught many of the breeding males and females during the breeding season. About half of the breeding birds have been raised in the nest-boxes in previous years, so that we possess considerable information on survival of the nestlings. Additional information on survival has been obtained by trapping birds at other times of year, outside the nesting season.

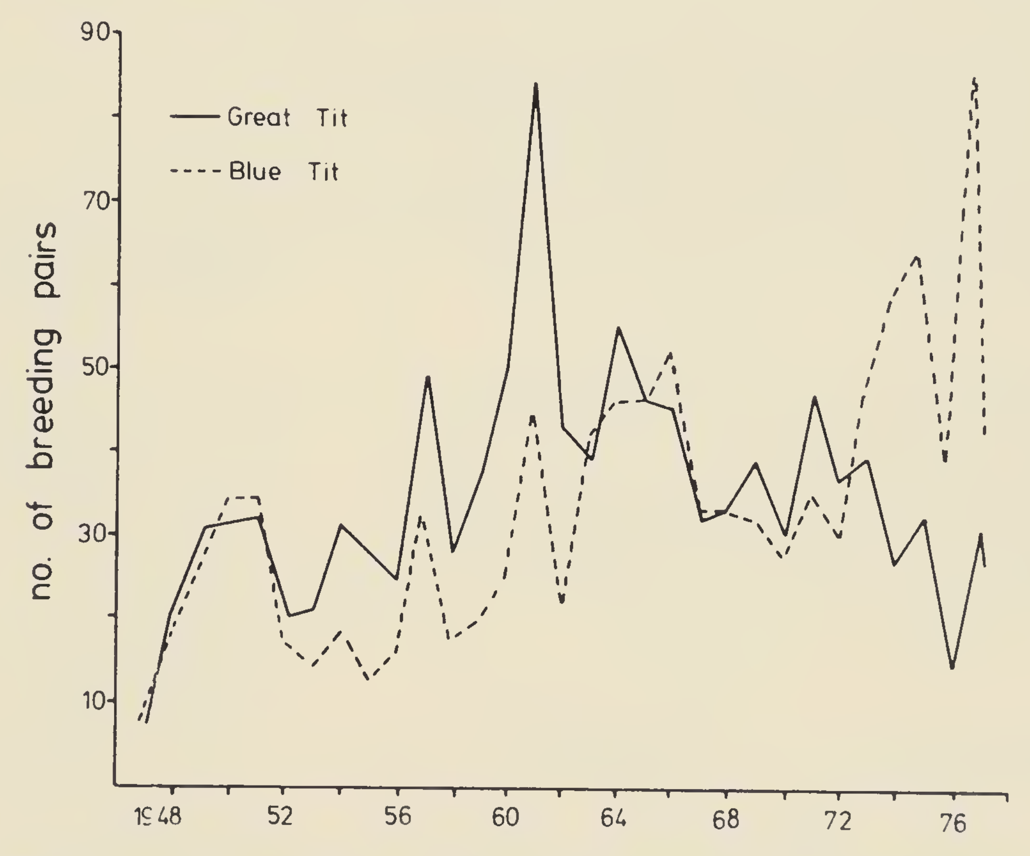


Figure 1. The numbers of breeding pairs of Great and Blue Tits in Marley Wood, Oxford, 1947–1978.

The number of breeding pairs of both Blue and Great Tits in Marley is shown in Figure 1. From this it can be seen that numbers are by no means stable, though on average the populations rarely change by more than a factor of two between years. Two main questions can be asked of such information and, although they are sometimes confused,

Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, Oxford OXI 3PS, UK.1

they are in fact quite different questions. One of these questions is "Why does the number of animals fluctuate around the levels that it does?" In other words, why are there usually between 20 and 40 pairs of Great Tits in Marley as opposed to only ten or more than one hundred. The other question is "What are the reasons for the year to year changes in numbers?" In other words, what is it about each individual year that results in a change in numbers? The factors producing the observed level are likely to be density dependent; those leading to changes in numbers, especially those that lead to deviations from the mean, may well not be, though they may contain a density dependent component.

My aim in this paper is to look at survival of individuals, especially young birds, within the population in relation to the year to year changes. In order to do this, it is necessary to summarise briefly the background knowledge of the main events in the annual cycle. This is done in Table 1. Potentially large differences in survival occur at a number of different times of year and these too are listed in Table 1. Any of these, or a combination of them, could produce variations large enough to bring about the observed year to year changes. Indeed, at one time or another, some author has suggested for some species that each of the features listed in Table 1 is the "key factor" responsible for population regulation of birds. Some of the main behavioural features associated with the regulation of Great Tit populations have been summarised recently by KREBS & PERRINS (1978).

TABLE 1: A summary of the major stages of the annual cycle of the Great Tit in Wytham Woods (from KREBS & PERRINS 1976)

Time of year	Stage of annual cycle	Possible adjustments of numbers
i Early spring (Jan. – March)	Territories are set up	Some birds are unable to obtain territories, and therefore do not breed, at least in good habitats
ii Late spring (April – May)	Breeding season	Clutches vary considerably in size, fewer eggs being laid at high density
iii Early summer (June – July)	Young birds leave the nest	Within two weeks they are mostly independent of their parents. Aggression between young birds is common; many young birds disappear
iv Early autumn (Sep.–Oct.)	Resurgence of territorial behaviour	Numbers remaining in an area may be adjusted. However, many young birds are not apparently involved, at least in English populations
v Late autumn (Nov.)	Winter population more or less stabilized	A very variable proportion of the summer's young are still in the population at this stage
vi Winter (Dec.–Jan.)	Shortest days for feeding. Birds moving around in mixed flocks. Some territorial behaviour in mild weather	Some mortality, but usually less than that preceding stage v

There are, I believe, two main problems about the Great Tit populations that have not been adequately explained. Firstly, we need to understand more fully the role of territorial behaviour with respect to population regulation. Secondly, we find that the post-fledging survival of the young is very variable and we cannot explain why this should be so. As we shall see, the two features, territorial behaviour and survival of the young, may be closely related.

The main features of the annual cycle of the Great Tit are described below.

Territory holders take up their territories

The number of breeding pairs which occupy territories at the beginning of the year varies markedly. Inasmuch as these birds occupy the whole of the wood (there is little or no space between the territories), it could be said that the territorial requirements of the individual birds affect the level of the breeding population. Such a suggestion is supported by the observation of KREBS (1971) who, by removing territory-holders and observing the territories being filled up again, showed that there were "surplus" or floating birds which were prevented from obtaining territories.

In fact not all the "surplus" birds are without territories; Krebs showed that, when he removed woodland territory holders, some of the replacements came from surrounding hedgerows where they too had held territories. One has to conclude that these birds preferred the woodland and were prepared to move quickly into it (often within 24 hours). Further, it seems that there may not always be large numbers of surplus birds alive in spring since the hedgerow territories were not re-filled (KREBS, 1971). However, in other years continued removal experiments yielded replacements (KREBS, 1977). These removal experiments were conducted in March; removals later in the season, in May, resulted in no replacements (WEBBER, 1975).

There are two unresolved problems related to these observations on territories. Firstly, as can be deduced from Figure 1, the size of territories varies markedly between years. Usually the wood seems to be completely filled by territory-holding birds and even at quite low densities (i.e. large territories) there seem to be birds that cannot obtain a territory. We do not know what proportion of the birds are unable to obtain woodland territories but, somehow or other, the territory holders "decide" to hold territories of different size in different years. Hence it is not clear how territorial behaviour and population density are linked.

The second problem may be simply the reverse of the first. As I shall discuss below, the number of breeding birds (and hence, again, the territory size) can be forecast, with some degree of accuracy, from the juvenile:adult ratio the previous autumn, high juvenile survival leading to high populations, low juvenile survival to low populations (PERRINS, 1965). Hence the size of the territories in spring appears to be determined by the size of the population the previous autumn. This is not to say that all birds can obtain a territory; it is possible that the higher the population, the greater the proportion which fail to obtain a territory. This argument is along the lines of the "rubber discs" first proposed by HUXLEY (1934) and would seem reasonable, but has not been demonstrated in the tits except perhaps in the sense that KLUYVER & TINBERGEN (1953) showed a buffer effect. However, in broad outline it seems that the number of young birds which survive to autumn (i.e. the

size of the population) is what, at least in part, regulates the size of the territories and we do not know what effect the territories have on the size of the population.

The history of the territories from year to year needs more study. On average, half the territory-holders survive from one year to the next and breed close to where they bred before (Bulmer & Perrins, 1973; Greenwood, Harvey & Perrins, in prep.). Hence, if they maintained the same territories exactly, half the wood would be available for subdivision between the new breeders. The way in which the established breeders and the new breeders subdivide this area has not been studied in sufficient detail. Hence we still do not know to what extent territorial behaviour limits the population.

In addition we still do not understand the advantage to the individual of having a territory. One result of territorial spacing may be to minimise the dangers from predation (Gibb, 1956) since the greater the distance between nests, the greater the chance of raising young (Krebs, 1970). In the case of our Wytham study, both Great Tits and Blue Tits nest in large numbers in the nest boxes and the spacing of one species in isolation from the other would not be very effective. Dunn (1977) has shown that the density (and hence the spacing) of the two species combined affects the predation rate. Currently we are studying the spacing of the two species and there is some preliminary evidence that the spacing of the two species is not independent of one another.

Breeding output

The breeding biology of the Great Tit has been studied in considerable detail. Variations in both clutch size and breeding success lead to large fluctuations in the numbers of young fledged per year.

In Wytham the mean clutch-size of the Great Tits has varied between 7.8 eggs (in 1951) and 12.3 (in 1948). The number of young produced has varied accordingly. The brood-size varies for a number of reasons. The adaptive nature of the clutch-size has been discussed in detail elsewhere (Perrins, 1965; Perrins & Moss, 1975). The success of the brood is related to the number of young in the brood, the age of the female, the habitat in which the territory is and, particularly important, the time at which the clutch hatches. All these features of any given nest reflect the amount of food each young bird will receive and hence its weight at fledging. The weight of a chick at fledging has a considerable effect on its chances of survival (Perrins, 1965).

More recently, it has become clear that there is at least one other factor which influences the weight of the young and this is the "ability" of the female. In another current study we are giving, artificially, broods of the same size to females which lay clutches of different size. The tentative conclusion is that the females which lay the larger clutches raise young which are heavier at fledging than those females which lay a smaller clutch (Perrins, in prep.). In other words, the females which lay the larger clutches are better able to raise young than the females which lay the smaller clutches. Hence females make a correct "judgement" about the circumstances in which they are breeding by laying a clutch which can be correlated with the amount of food that they can bring to their young. Whether the "ability" of the female to raise young relates to her own physical quality, to the quality of the male (as shown for example by Nisbet, 1973, 1977), or to some micro-habitat feature of the immediate surroundings of her nest is not known. Whichever is true, the female

must be able to recognise, and respond to, the necessary features. If the current tentative findings are upheld by further results, the correlation between the individual female's ability and her clutch-size is a factor which must be taken into account in analyses of optimum clutch-size.

Although the weight at fledging strongly affects the survival rate of a young Great Tit, the date at which it hatches is extremely important also. The earlier the young are raised, the greater their chances of survival. Although the weight of fledglings usually declines as the season progresses, the effect of date seems to be important in its own right. Comparing chicks of equal weight, survival is higher for those which hatch earlier. In some cold springs, early-hatched young have fledged at lighter weights than later ones (because of low temperatures, the female had to spend more time brooding the young and so only one parent, the male, could feed them); nevertheless the subsequent survival of the early young was greater than that of the later ones. The earlier broods are so much more successful than later ones that one wonders why all the birds do not breed earlier (PERRINS, 1970). One of the more interesting findings is that the laying date of an individual is related to its body size (JONES, 1973; GARNETT, 1976), the smaller birds breeding earlier (Fig. 2). Hence, for this feature of the life cycle, selection favours smaller individuals. I shall return to the size of individuals later.



FIGURE 2. Relationship between the winter weight of female Great Tits and their date of laying with respect to the population mean.
$Y = 1.65 (X) - 30.96$
$r = 0.368$
$n = 130$
$p < 0.001$
Filled circles – data from JONES (1973)
Open circles – data from GARNETT (1976)

The number of young raised is not only related to variations in clutch-size; the proportion of successful nests also varies considerably. The main reason for this is a highly variable predation rate. Predation of eggs or young is mainly by weasels, *Mustela nivalis*, and the situation has been described by DUNN (1977). The number of nests lost to weasels is, as discussed above, partly a response to the density of the tits, but also partly a response to the density of small mammals which are apparently the weasels' preferred prey.

In Continental Europe there is a further factor that affects the productivity. In contrast to those in deciduous woodland in Britain, many Continental Great Tits have second broods; more than 30% of the pairs raise second broods in deciduous woodland in some years. Amongst other factors affecting the probability of having second broods, there is a strong inverse correlation with breeding density (KLUYVER, 1951). One result of this is that

on the Continent more young are raised per pair than is the case in Britain. As a consequence, and because adult mortality is similar in the two areas, juvenile mortality must be correspondingly higher on the Continent than in Britain. One is tempted to speculate that competition between different individual young must either be more intense on the Continent than in Britain or occur at additional periods of the year.

TABLE 2: Effects of density dependent variation in clutch-size on subsequent population change

Population in year 1 (pairs)	C/S	No. eggs + adults	No. surviving*	Total	% change
10	11	110 + 20	11 + 10	21	+ 5 %
80	8	640 + 160	64 + 80	144	− 10 %

* Table assumes all features of the population are constant except clutch-size. Survival rate of eggs to breeding birds is taken as 10 %, that of breeding birds as 50 %; both figures are close to the average observed.

Although the number of young raised (measured either as the number raised per hectare or as the number raised per pair) may thus vary quite markedly, production does not relate in any obvious way to the changes in breeding numbers between any two years, i.e. no correlation has been shown between productivity in one year and changes in breeding numbers in the following year. As a result of this, it has been suggested that the variations in breeding output between years could not have a regulatory effect on the population (LACK, 1966). Such large year to year variations in post-fledging survival occur that they tend to swamp the smaller changes that precede them. In particular, although at least three of the factors affecting reproductive output are density dependent (clutch-size, proportion of second broods and predation) the lowered reproductive output as the breeding population increases does not compensate for the increase in population with the result that there are more tits raised per hectare at times of high density than at times of low density. Nevertheless, KREBS (1970) showed that changes in breeding output can have a regulatory effect. This can come about because of the differences between the survival rates of adults and young birds. Table 2 shows the population change resulting from variations in clutch-size alone; all other features are constant. In the case of the higher population, too few young survive to replace the adults which die and so the population declines. In the lower populations more young survive than adults die so that the population increases.

Hence the observed changes in clutch-size can have a regulatory effect on the population.

Post-fledging survival

We have been able to establish relationships between features of the nesting period and subsequent survival by extensively trapping the birds during the winter. Great variation in survival between leaving the nest and reaching the winter is found in most study areas. In Wytham, as many as 2.0 young/old bird and as few as 0.16 young/old bird have been found alive by the late autumn – a greater than 10-fold difference. The differential in survival is important since the proportion of young reaching the autumn appears to be the best indicator of year to year changes in breeding numbers (PERRINS, 1965). This is the "key factor" in the annual changes in the Great Tit.

One of the gaps in our study is that we have not been able to follow the young in detail through the few months after fledging when these large changes are taking place. At this time they stay in the tree-tops and are not easily caught. However, WEBBER (1975) succeeded in establishing a certain amount about the birds during this important period of their lives. In particular, he showed that many of the juveniles caught within two to three weeks of leaving the nest had lost weight; some of them were considerably lighter than they were when they left the nest. He was not able to show that fledging weights affected survival during this time, but his findings support the suggestion that this may be a difficult time for the young birds.

In spite of the lack of knowledge during this period, it is clear that the majority of the young birds have "disappeared" by the end of the autumn (October/November); normally the juvenile:adult ratios of birds trapped through the winter show little change after this date. The reasons for the variable and sometimes very high post-fledging disappearance are not fully understood, but two main suggestions have been made. Firstly, KLUYVER (1951) suggested that most of the birds that disappeared during this period had in fact emigrated rather than died and that they did this late, in early autumn, in response to social pressures arising from the autumn resurgence of territorial behaviour shown by the adult birds.

There are obvious problems associated with attributing the disappearance of birds to emigration (since most tit populations seem to have synchronous changes in numbers, the emigrants cannot be contributing to other populations; at best they must be emigrating to marginal habitats for the species and dying there). More recently KLUYVER (1971) produced some very important experimental work to show that the chances of a young bird settling in a given area are related to the number of other young that have already settled there. KLUYVER's results clearly demonstrate some form of interaction between the young of early and late broods, with the advantage going to the former. They do not demonstrate the mechanism of the interaction, neither do they indicate the precise time at which it occurs.

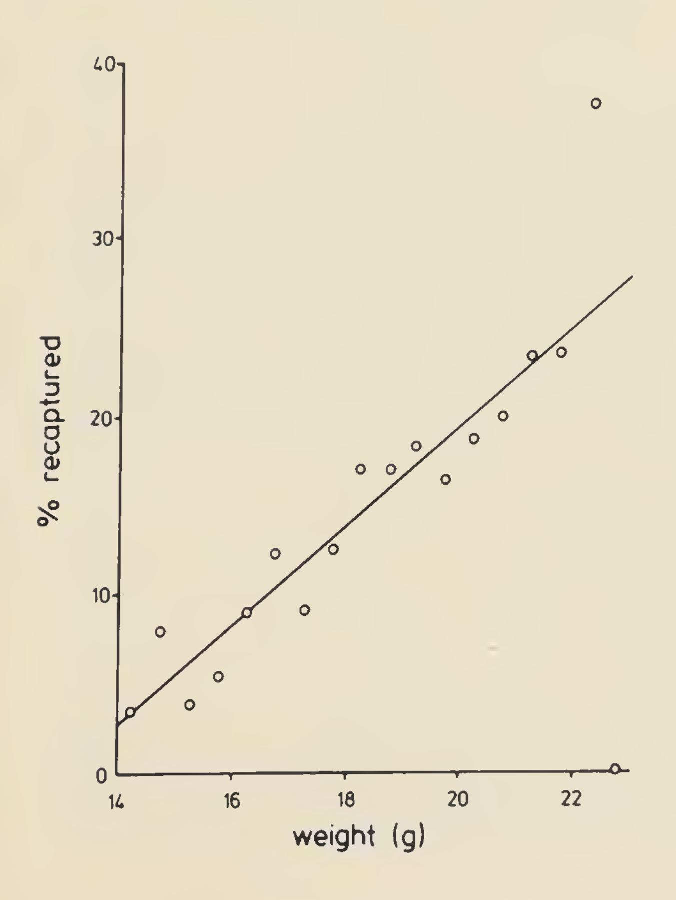


FIGURE 3. Relationship between recapture rate and fifteenth day weight when all years combined (from MOSS, 1972).

TABLE 3: Proportion of variance in fledging weight explained by weights of body components (from GARNETT 1976)

(1) Lean dry carcass weight	57.9%
(2) (1) + Lean dry weight of pectoral muscle	80.5%
(3) (1) + (2) + Total fat	89.2%

I proposed a different explanation for the variable disappearance of the young during the late summer period (PERRINS, 1965). My suggestion was that the newly fledged young encounter variable conditions for collecting food during the very difficult period when they are learning to feed for themselves. I noticed that there was a close correlation between fledging weight and survival in Wytham (Fig. 3). I suggested that the heavier birds were carrying greater fat reserves and that the greater the fat reserves the greater the chance that a young bird would survive the difficult period just after fledging when it was learning to find food for itself. In two years I colour-ringed the young birds by their weight class and found that, within a month of fledging, there was already a difference between the weight classes: more of the light than of the heavy birds had disappeared.

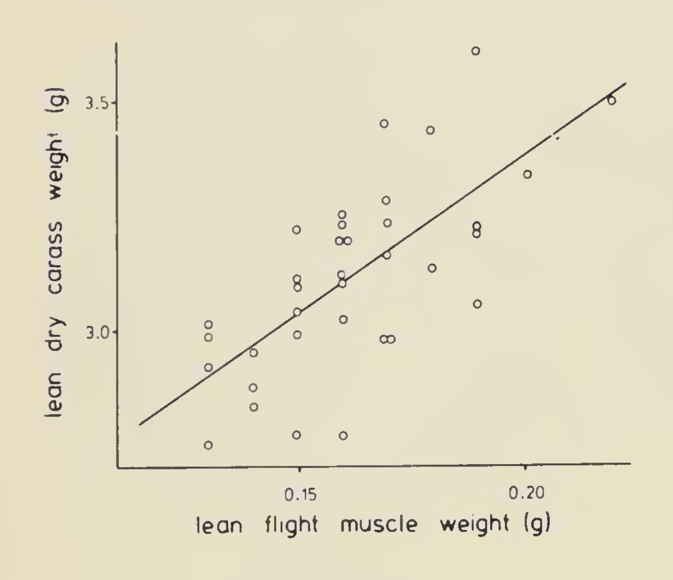


FIGURE 4. Regression of lean dry carcass weight on lean dry pectoral muscle weight.
$Y = 6.74 (X) - 2.02$
$r = 0.677$
$p < 0.001$
(from GARNETT, 1976)

In a more recent study, GARNETT (1976) has examined certain aspects of the body-size of young Great Tits. He showed that fat does not contribute greatly to the weight differences between young (Table 3). Compared with lighter young, the heavier young tend to have longer tarsi, larger pectoral muscles and a higher lean dry weight (Fig. 4) but only slightly more fat; they are "larger" birds (Table 3). Further, there is a strong correlation between the fledging weight and the winter weight, and between the tarsus length at fledging and the tarsus length in winter (Fig. 5), showing that birds which are larger at fledging remain larger for life. (Although there is a tendency for males to be larger than females, this correlation is true within each sex.) Garnett was also able to show that, as one might expect, body-size included both heritable and environmental components. Garnett went on to examine the behaviour of newly fledged Great Tits; he studied, in the aviary, small parties of birds made up of individuals of different weight. Within a week of fledging, aggression was apparent, with the heavier birds dominating the lighter ones.

Many questions remain to be answered about the survival of young birds in the summer, but a pattern does begin to emerge. The young which are better nourished while they are in the nest leave the nest larger than those which are less well nourished. In later interactions

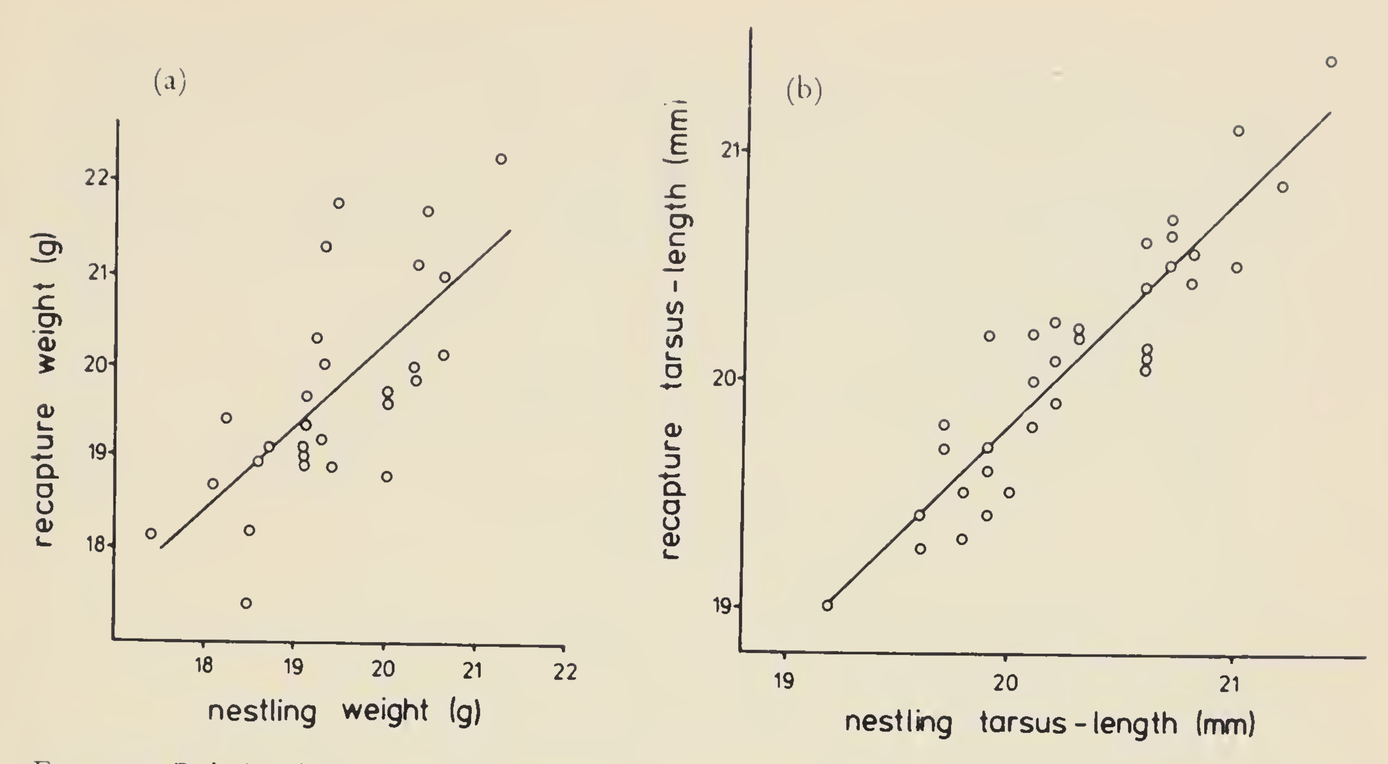


FIGURE 5. Relationship between (a) Nestling weight and weight when recaptured in winter ($Y = 0.937 (X) + 1.51$; $r = 0.715$; $p < 0.001$) and (b) Nestling tarsus length and tarsus length when recaptured in winter ($Y = 0.983 (X) + 0.151$; $r = 0.917$; $p < 0.001$) (from GARNETT, 1976).

the former dominate the latter who either leave or, more probably, die. In the same way, birds raised earlier in the season are at an advantage over young raised late in the season.

We still do not know when most of the losses take place. WEBBER (1975) analysed the Wytham data in an attempt to discover a critical period in the summer when the young died. He showed that there was a decline in the number of juveniles in the population throughout the period from fledging in June to October (Fig. 6). Although as many as 60% of the young might die during the period prior to August, there was no clear evidence in favour of either my suggestion of theat of KLUYVER; there was no obvious time of exceptionally high mortality. Such a view is supported by recent analyses of British ringing data for the Blue Tit, where again there is no month during which mortality is strikingly higher than in others (Perrins, in prep.). In both species winter mortality of juveniles appears to be no higher than that for adults, at least after about November or December, confirming the view that juveniles survive as well as adults after this date. The slight dip in the line in Figure 6 between March and the breeding season is probably explained by the fact that a small proportion of the first year males fail to find a mate because of an unbalanced sex ratio (BULMER & PERRINS, 1973); the breeding season sample is based wholly on breeding birds and hence non-breeding males are not sampled.

I want now to discuss what I regard as the major puzzle about population changes in the Great Tit, namely the variation in survival of the young.

Firstly, as I have shown, we know several factors which affect the individual's chances of survival after it has left the nest. In a statistical sense, we can rank them by their weight at fledging. Such a ranking can be made with a high probability of success since heavier young are more likely to survive than lighter ones. However, while we can fairly accurately predict which individual fledglings are more likely to survive than others, we cannot at present predict what proportion of the fledglings will survive; it may be many or

it may be few. Since the number which survive is so variable and has such an important effect on the annual changes in numbers, this is an important omission. In addition, there is an implication which has not been fully examined. In an earlier paper, I showed that in years when very large numbers of the young survived, this was because an unusually high proportion of the lighter young survived. In view of Garnett's findings it seems likely that in these very favourable years it is not birds with low fat reserves that survive but rather birds with small body-size.

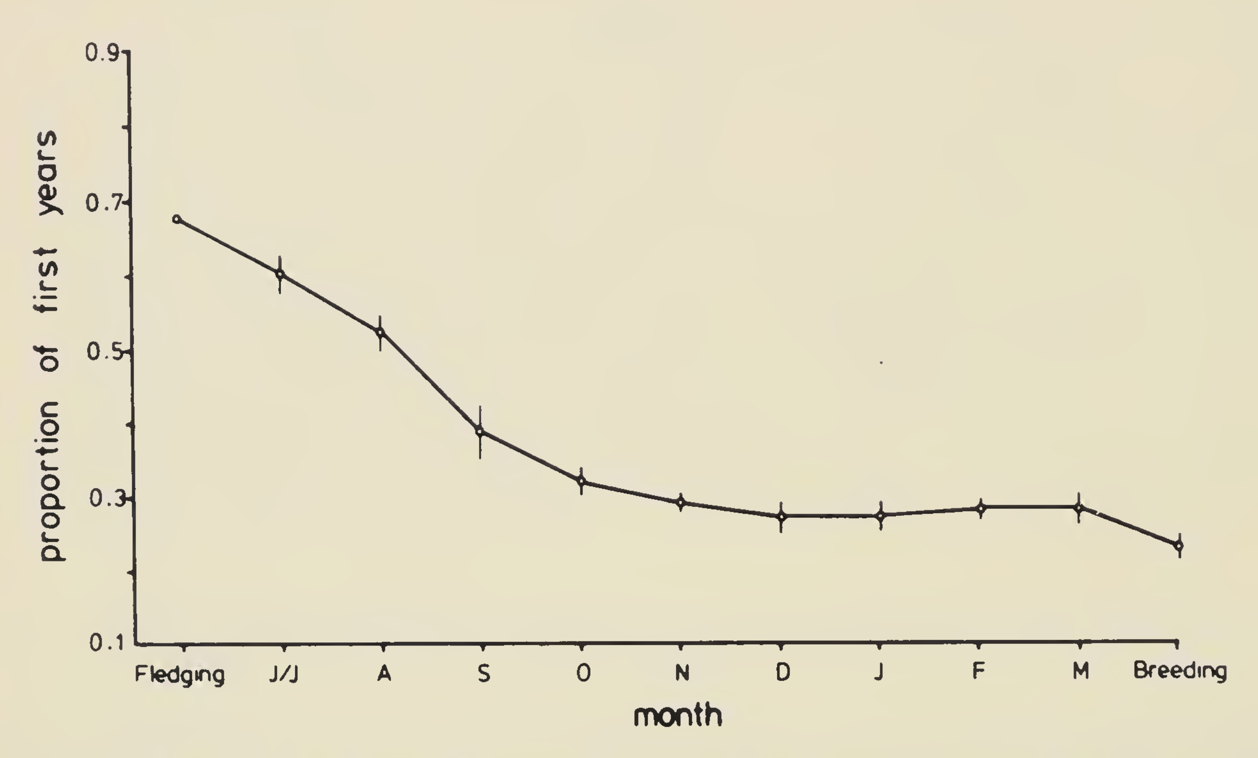


FIGURE 6. Proportion of the resident population (Wytham-born young + breeding birds) made up of Wytham-born young. Data are plotted against month and are averaged over the years 1961–74. The first three points are not spaced at equal intervals so that the slopes of the lines cannot be relied upon for comparisons of mortality (from WEBBER, 1975).

We have only one clue to the factors associated with the variable survival. There is a strong correlation between the proportion of the young which survive and the size of the beech crop (*Fagus sylvatica*) in the autumn of that year (PERRINS, 1966). Plainly, the beech crop is a very important food source for the tits during the winter; they may feed on it almost exclusively throughout the winter. However, for a variety of reasons it seems unlikely that the relationship is a simple, direct one. The most important of these reasons is that the birds do not feed on the beech crop in any numbers until November or December, by which time the major mortality of the young has occurred in most years. Hence the mortality of the young tits appears to "predict" the winter seed crop, being high when seed crops will be low and vice versa.

At present we have no understanding of how this association comes about, but there are a number of known correlations with the beech crop which shows that a biological connection between features which occur earlier in the year and the beech crop is possible. For example most forest trees which fruit irregularly tend to crop synchronously (MATTHEWS, 1963); some of these ripen earlier in the year. Even those species which crop annually tend to have heavier crops in the years when the trees which crop irregularly have their crop (HYDE, 1967). Trees put on less wood in years when they are producing fruits

(ROHMEDER, 1967; HARPER, 1977) and, in addition, the levels of at least nitrogen, potassium and starch in trees tend to vary with whether or not they are producing seeds, being low in years of seed production (HARPER, 1977). What effect, if any, this has on most insect populations is not known, but the sycamore aphid, *Drepanosiphon platanoides,* is affected by the quality of the leaves of the sycamore, *Acer pseudoplatanus* (DIXON, 1970).

Hence, considering the lack of knowledge in this field, there is a very real possibility that there is some feature of the environment which directly influences the survival of the young tits just after fledging and which is correlated with years of good seed crops which occur later in the year.

Emigration/Immigration

There is little evidence as to whether or not the movement of birds can be related to the changes in numbers. WEBBER (1975) was unable to show that emigration was density dependent. In any case it seems to be less frequent than in Continental studies and less related to fledging date. Similarly WEBBER showed that immigration seemed to be at a fairly constant rate and not related to the number of birds in Wytham.

We do not know the origins of the immigrant birds and, since about half of the Great Tits which breed in our study area were themselves raised in the nest boxes, this amounts to half our breeding population. However, we have recently acquired one piece of indirect evidence about the immigrants. We have measured the dispersal distance (between birth-place and breeding place) of males whose fathers were also born in the wood. There is a correlation between the distance moved by a father and his son (GREENWOOD, HARVEY & PERRINS, 1979). One might expect that immigrants would have a greater dispersal distance than residents and that their offspring would inherit such a tendency to have similar dispersal distances. However, the dispersal distance for the sons of immigrant fathers is the same as that for sons of Wytham-born fathers. Although the measurement is biassed (since birds dispersing long distances are not encountered) we believe this analysis shows that the immigrants to our breeding population are of the same local populations and so must come from hedges and woods close by.

The situation in Britain may be different from that on the Continent. There are two reasons for this suggestion. Firstly, most Dutch birds that have been shown to emigrate were reared in late broods, mostly second broods, and as we have seen, such broods are rare in Britain. Secondly, compared with data in KLUYVER (1971) there is a significantly lower number of Wytham recoveries over 25 km from their birth-place (20 out of 1,369 in Holland, 7 out of 2,028 for Wytham; $X^2 = 11.7$, $p < 0.001$).

Emigration may be more common in Continental populations than in British ones, but I find it hard to believe that, in the latter at least, it has a marked effect on the population. This is partly because of the synchrony that is observed between changes in numbers in different populations and partly because of WEBBER's finding that immigration into Wytham is independent of the Wytham population density.

Winter survival

At first sight, one might imagine that the vagaries of the winter weather would have a major influence on the survival rates of a small bird such as a Great Tit. Indeed, in Finland,

there is a good correlation between breeding numbers and winter temperatures (Von Haartman 1973). However, in Wytham the winter is less severe than in Finland and the weather seems to exert a less powerful influence on survival.

It remains slightly surprising to me that we cannot show a correlation between winter survival of adults and the weather as was shown by Von Haartman. During the period of our study, there was one extremely severe winter (1962–63) with snow cover for about 10 weeks and very unusually cold weather. The adult survival rate from the breeding season of 1962 to that in 1963 was over 60 %, an unusually high figure. The reason for such good survival in such extreme conditions appears to result from the good beech crop which coincided with the hard weather. Another very hard winter preceded the start of the study when only 7 pairs bred (as opposed to a normal 20–30). In this year there was no beech crop and hence one is tempted to suggest that a hard winter does result in high mortality, but only if food is scarce.

There is one further problem relating to the survival during the hard winter of 1962–63. In the autumn of 1962, there were very large numbers of juvenile Great Tits in the wood. We anticipated a great increase in the breeding population the following year. This did not happen and yet, as we have seen, adult survival was not unusually low. It therefore seems likely that the juveniles, but not the adults, suffered an unusually high mortality during that winter. Differential survival between adults and juveniles after about December seems unusual, again suggesting that winter weather is not normally a factor which has an important effect on winter survival.

There is a weak correlation between the annual survival of breeding females and the survival of the young birds, suggesting that adults and juveniles do show parallel changes in survival (Webber, 1975). It seems most likely that this correlation arises from the slightly higher survival of adults in winter with beech crops than in winters without crops.

Discussion

Population regulation

One of the difficulties of working with the Great Tit populations is that they show large year to year variations. These, at least when they move the population away from its average level, are presumably density independent; most of the large increases are associated, in some way, with the beech crops. Any attempt to demonstrate density dependent features of the annual cycle (which presumably exist, but may be quite small) is almost certain to be unsuccessful against a background of such large presumably density independent variation.

In some ways the Great and Blue Tit are atypical of the Paridae, at least of the other members which have been studied in any detail. These two species in deciduous woodland have territories of about one hectare; in years of high density territories may be only a half or even a third of a hectare. Most other species hold much larger areas. The Marsh Tit *Parus palustris,* Coal Tit *P. ater* and Black-capped Chickadee *P. atricapillus* in their most favoured habitats have territories of between 4 and 6 hectares, while territories of the Willow Tit *P. montanus* and the Crested Tit *P. cristatus* are larger.

In at least some of these species the autumn territories have a more obvious possible value than in the Great and Blue Tit. Many of these other tits live almost exclusively in

their territories throughout the year. In these tits, but not the Blue or Great Tit, the birds store much food during the late summer and autumn (HAFTORN 1953 et seq., 1960) and take much of this again later in the winter. The survival value of a winter territory – and hence of autumn territorial behaviour – is more obvious in such species. In some, the winter territory is defended by more than a single pair, though the group is usually reduced to two by late winter, apparently by death (EKMAN, in prep.). Surplus birds are either few or have very low survival rates since replacements after spring removal may not occur. Indeed by spring in northern populations, unmated males and vacant territories testify that there are no surplus birds.

The annual cycle of the Great Tit, depicted in Table 1, is similar to that for a great number of temperate species, both passerine and non-passerine. Although many of these species maintain more stable numbers than is the case with Great Tits, there is little reason to suppose that the basic pattern of the factors controlling their life cycle is very different.

One well-studied species is the Red Grouse *Lagopus lagopus*. This bird has an annual cycle basically similar to that of the Great Tit. It has annual changes in numbers in which, again like the Great Tit, numbers of breeding pairs tend to be high (i.e. territories small) after high survival of the juveniles in the previous year (WATSON & MOSS, 1972). Work on this species has shown a number of inter-acting correlations around the year, with varying food quality being implicated as one of the factors resulting in population changes (MOSS & MILLER, 1976). It is only fair to stress that these authors interpret the annual changes differently from the way I have interpreted the annual cycle of the Great Tit.

However, other workers have shown that the young grouse, which again like the Great Tits have a very variable survival, are also dependent to a considerable extent on a diet of insects (BUTTERFIELD & COULSON, 1975). Variations in the abundance of insects might well be critical for the survival of the young grouse. Hence, although it is a very different sort of bird, there are some problems potentially similar to those for the Great Tit in understanding the population dynamics of this species.

The size of individuals

Another aspect of bird populations that we know very little about is the relationship between fitness and body-size. In the case of the Great Tit, we are beginning to collect a certain amount of information about the advantages and disadvantages of birds of different size. I am not concerned here with the factors which act between populations resulting in different sizes of birds in different places, e.g. Bergmann's rule, although such differences have been demonstrated with Great Tits (SNOW, 1954). Obviously, since most organisms are not changing rapidly in size, natural selection in some way acts against individuals of extreme size. The selective advantage of animals of different size may well be different at different times of year. Such appears to be the case in the Great Tit and one can begin to see some of the forces that act on the individuals within a population.

Within the Wytham population, certain features related to body-size are known. Large size, which is partly an inherited and partly an environmental effect, is important to a bird in a number of ways. Large birds lay larger eggs than small birds; the young hatching from large eggs grow faster and may have higher survival than birds from smaller eggs (SCHIFFERLI, 1973). In competition with their siblings for food, larger young may be at an advantage. Once they have left the nest, larger young have a higher survival rate than

smaller ones, perhaps in part because they dominate the smaller ones. The same may be true in winter when again larger birds are dominant at food sources. In addition to being at an advantage in contests over food, larger birds suffer less metabolic stress when the temperature drops sharply (KENDEIGH, 1969); they also tend to be able to store proportionately more food reserves than smaller birds and this too may put them at an advantage in adverse conditions.

Nevertheless, the large bird does not have all the advantages; small birds are at an advantage in a number of ways. Although it has a higher metabolic rate per unit of body weight, a small bird needs, overall, less food than a large bird and hence, other things being equal, is at an advantage. If small birds are feeding in close proximity to larger birds (and especially if they are taking large items such as beech mast), they are likely to lose food as a result of aggressive encounters; the overall advantage is then with the large bird (GIBB, 1954; GARNETT, 1976). If, however, the food items are small or the birds too dispersed for feeding interactions, the small birds are at an advantage; they need less food and can apparently gather it as quickly as large ones.

The advantages of being small are most clear in spring. The females require, in addition to energy for their own body maintenance, extra energy in order to be able to form eggs. Assuming that all birds have an equal feeding efficiency, and that the food supply increases prior to breeding, the smaller females, needing less energy to maintain themselves, will reach the required level for breeding sooner (PERRINS, 1970). While some of this argument is hypothetical, small female Great Tits breed earlier than larger ones (Fig. 2) and gain a considerable advantage from doing so; their young survive better as a result.

In view of the fact that the young raised by the early-breeding females tend to be small (for genetic reasons) one might expect them to be at a disadvantage in competition with larger young of later broods. This does not appear to be the case in mid-summer for, although early young may leave the nest at a lower weight than later young, they always seem to be at an advantage over the later young. One is tempted to infer from this that the critical interactions between the young occur fairly soon after fledging when the low weight of early young is compensated for by their greater experience and development; but there is little evidence on this point.

Body size at fledging is clearly important to the survival of the young birds. As we have seen, it is not known exactly when the larger birds gain this advantage over the smaller ones. However, the birds that were heavier at fledging do not appear to be at an advantage over the smaller birds after the autumn. We have large samples of birds which have been trapped in winter, but have not been caught breeding; presumably most of them died before the breeding season. The fledging weights of these young are not distinguishable from those of young birds which are known to have survived to breed. This is true for both males and females. Hence although we know the birds are still of different sizes, there is no disadvantage in being small in winter. All selection against small birds seems to take place some time in the first few months after fledging. Thereafter, the only major advantage we know of is that small females are at an advantage over large ones in the breeding season.

Hence, as one might expect, there is a balance between being large and being small. If this is the case, one might expect the balance to shift between years, at least at times. For example, very high juvenile survival in part results from a greater number of the smaller young surviving than is normally the case. Similarly, mild winters might result in smaller

birds showing a higher than usual survival. Either of these cases would lead to both high density and a slightly smaller mean size of Great Tits. This has not to my knowledge been shown, but I would predict that it should be so.

Summary

Factors affecting population size in the Great Tit are discussed. Two stages of the annual cycle seem particularly worthy of further study.

The number of young surviving from fledging to the autumn varies greatly. The reasons for this are unknown, though they are in some way correlated with the years in which there are good crops of seeds, especially of the beech. The proportion of young which survive to autumn is the most important factor influencing population change.

The role of territorial behaviour needs to be examined more fully. Inasmuch as high juvenile survival leads to high population levels and small territories, it appears that survival is more important than territorial behaviour in influencing population change. However, territorial behaviour does result in the exclusion of some birds at least from the best habitats, but the proportion which is excluded under different conditions is not known.

At different times in the annual cycle birds of different body size are at an advantage over birds of other sizes. Large body size is advantageous after fledging; many more of the large birds survive than the small ones. Either large or small birds may be at an advantage in the winter depending on the conditions prevailing at the time. Small females lay earlier in the spring than large ones and, since early breeding is advantageous, produce more surviving young.

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SYMPOSIA

Volume I

Volume II



SYMPOSIUM ON FUNCTIONAL AND ECOLOGICAL MORPHOLOGY THE ANALYTIC ANALYSIS OF AVIAN ADAPTATIONS

9. VI. 1978

CONVENERS: WALTER BOCK AND VINZENZ ZISWILER

How are Morphological Features Judged Adaptive

WALTER J. BOCK

Introduction

Numerous ornithologists have discussed morphological features as adaptations or have speculated on the possible adaptive evolution of taxonomic characters. Yet, few of these workers have indicated the methods used to judge the adaptive nature of morphological structures or how a particular evolutionary change is shown to be an adaptive one. In this symposium, we are not concerned with the demonstration of particular avian adaptations, but with the sequence of studies needed to judge the adaptive nature of morphological features and with the use of these conclusions in further ecological, taxonomical and evolutionary work. Each contributor will discuss, with examples, an aspect of the analysis needed to determine an adaptation; the entire analysis is provided by the symposium. Although we will discuss only morphological features, the suggested methods are general and should apply to all biological features.

What is an adaptive feature

The concept of adaptation is an old one, predating not only the development of evolutionary theory but also the beginnings of biological science. It has always been used to indicate biological features which permit the organism to exist successfully in a particular environment. Thus, the avian wing is an adaptation to an aerial environment, webbed feet to an aquatic environment and so forth. Evolutionary theory was developed largely as an explanation for the origin and further specialization of biological adaptations.

An adaptation is thus a phenotypic attribute of an organism and is always judged with respect to a particular selection force of the environment. The biological feature and the environmental selection force must be specified precisely when describing an adaptation. To say that the wings of penguins are an adaptation is meaningless because being adapted is not an intrinsic property of a feature, such as its mass; being adapted is a relative property. It is essential always to state the selection force to which the feature is an adaptation. Wings of penguins are adaptations to locomotion (swimming) in an aquatic environment.

Adaptations are judged relative to the external environment of the organism, and precisely to selection forces arising from the external environment, not to other parts of the individual organism. Muscles are not adapted to bones, but both are adapted to particular selection forces of the environment.

The phenotypic feature is the adaptation which requires a careful description of all aspects of the feature. It is the wing that is the adaptation, not just the morphology of the wing. Both the form (i.e. the morphology) and the functions (i.e. the physiology) of the feature must be described as a prerequisite for judging the adaptiveness of a feature (BOCK & VON WAHLERT, 1965). To speak about morphological adaptations, phys-

Department of Biological Sciences, Columbia University, New York, NY 10027, USA.

iological adaptations, behavioral adaptations, is not valid except as a shorthand indication of the research interests of the workers.

To be an adaptation, the feature must have a biological role, i.e., used by the organism in the course of its life history. The biological role interacts with a selection force arising from the environment (Umwelt) of the organism with the link between the biological role and the selection force being the synerg. A clear distinction must be made between the concept of function and that of biological role (Bock & von Wahlert, 1965; Bock, 1979) for a proper evaluation of adaptation.

An adaptation can be defined as a feature having properties of form and function which permit the organism to maintain successfully the synerg between a particular biological role of that feature and a specific selection force. By successful, I mean that the individual organism survives as an individual and reproduces to leave progeny. Adaptations must be judged on a probability basis and always against present environmental conditions, never against future ones. Success is a relative term and some measure of success or of the degree of goodness of the adaptation is needed. This can be done by a measure of the amount of energy required by the organism to maintain the synerg with better adaptations requiring less energy. Adaptive evolutionary changes are those which reduce the amount of energy required by the organism to maintain successfully the synerg (Bock, 1979).

Adaptation is a concept applied to individual features of an organism; it makes no sense to apply it to individual organisms or to the species. Adaptation is not equivalent to fitness, a concept applied to individual organisms. Rather adaptation is linked to fitness in that current evolutionary theory postulates that individuals with better adapted features will have the greater fitness.

Preadaptations are those features that possess properties of form and function permitting them to acquire an adaptive nature, but the needed biological role and selective force have not yet arisen (Bock, 1959; 1979).

Paradaptation refers to those aspects of features that are "besides adaptation". These are aspects of features whose existence can be attributed to the mechanisms of genetical variation responsible for the origin of new phenotypes (Bock, 1967) and hence comprise the total set of all aspects of biological features of which adaptations form a subset. Many differences observed between features when making a horizontal comparison are paradaptive, not adaptive.

Recognition of an adaptation

Close reading of the literature on adaptive features reveals several general methods used to ascertain adaptations. These may be categorized as the comparative, the correlative, and the synthetic (direct study) methods. Only the last is valid (Bock, 1977 a).

The comparative method depends on the assumption that morphological similarity indicates adaptive similarity and hence that each morphology (form) has a unique adaptive meaning. Thus, when attempting to determine the adaptiveness of a feature, one compares this feature morphologically with those of known adaptive significance. If the features agree in morphological form, then they agree adaptively and vice versa. Numerous examples can be given to show the erroneous basis of the comparative method (Bock, 1977 a).

The correlative method depends either on a correlation between two or more morphological features or on a correlation between a morphological feature and an environmental factor. The former does not provide any information an adaptation because it only shows relationships between two or more morphological features. Correlations between a morphological structure and an environmental factor are more promising, but correlations are only that and while they may indicate causal relationships, a correlation in itself is not a causal relationship. This must be demonstrated even after the correlation may be established.

The remaining method —the synthetic— is the only valid one. It depends on study of all aspects of adaptation from the morphological form to the environmental factors and hence requires a combination of laboratory and field studies (Bock, 1977 b). The major components of the synthetic method for ascertaining adaptations are the subjects of the several contributions to this symposium.

The synthetic method

The essential steps of the synthetic method may be summarized as follows:

a) Description of the morphological form which must be done with a clear understanding of the relationship between functional and structural properties so that the form is properly described.

b) Description of the functional properties based on experimental methods, together with the formulation of causal models for the observed actions, and etc.

These first two steps constitute the laboratory phase of study.

c) Description of the biological roles based on observations of how the organisms use their features in the course of their life histories.

d) Description of the environmental factors and of the selection forces arising from them so that the synergical relationships can be ascertained.

These next two steps constitute the field phase of study.

e) Determination of the adaptation based on all of the information gathered in the above studies and judgment of its degree of goodness by measuring the amount of energy required to maintain the synerg or by some other appropriate measure.

None of these steps can be omitted, each is essential for the determination of an adaptation. Unfortunately, few studies exist in avian biology which are complete or sufficiently complete to permit a realistic judgment of particular adaptations. In most morphological studies, no or insufficient attention is given to field studies, behavior and ecology. The last two decades have been fruitful ones in terms of a great development of functional morphology. Such studies constitute an essential, but not a sufficient part of adaptational investigation.

The major problem in adaptational investigations is they require a broad spectrum of work that is almost impossible for a single person to master. Who can become a descriptive morphologist, master the complex techniques of function anlysis, learn behavior and the multiple facets of ecology? A reasonable solution to the breadth and depth of study required on adaptational study is to establish informal teams of two or more workers. The minimum team should consist of a laboratory worker to undertake the descriptive and functional morphology and a field worker to do the behavior and

ecology (Bock, 1977 b). The essential factor of such teamwork is active feedback between each worker during the entire study. It is not possible to do two separate investigations and combine the results at the end if one hopes to ascertain the adaptive nature of the feature.

The beauty of adaptational analysis is that it encompasses the entire spectrum of biological studies. Such work, more than any other, can help serve to unify the current diversified field of avian biology.

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Zur Methodik funktionsmorphologischer Untersuchungen

PAUL BÜHLER

Einleitung

Das Ziel der Funktionsmorphologie* ist die Aufklärung der Beziehungen zwischen der Form und Struktur eines Organismus und den physikalisch-chemischen Gesetzmäßigkeiten, die das Funktionieren des Organismus ermöglichen. Funktionsmorphologische Befunde beziehen sich wie andere physiologische Befunde auf allgemeinbiologische Gesetzmäßigkeiten, und haben als solche ihren Wert, wenn sie neue und interessante oder gar überraschende Fakten und Zusammenhänge sichtbar machen — und in akzeptabler Weise erarbeitet wurden. Erstaunlicherweise findet man aber in der funktionsmorphologischen Literatur außer akzeptablen Befunden, die entsprechend den methodischen Grundsätzen der Naturwissenschaften erarbeitet wurden, relativ viele Angaben, die sich bei genauerer Überprüfung als falsch erweisen. Das Ziel dieser Abhandlung ist es, an Hand von einigen Beispielen aufzuzeigen, wie solche Fehlleistungen sich vermeiden lassen. Da der Autor sich selbst mit der Funktion von Kieferapparaten beschäftigt (BÜHLER 1977), wurden als Beispiele funktionelle Details der Kieferapparate von Vögeln gewählt. Um das Vorgehen bei der funktionsanalytischen Tätigkeit zu veranschaulichen, wurden außerdem die wesentlichen Schritte der funktionsmorphologischen Arbeit in einem Diagramm (Abb. 1) zusammengefaßt, auf dessen Einzelheiten im Anschluß an die Beispiele eingegangen wird.

Beispiele

1. LUBOSCH (1929) kommt auf Grund seiner Untersuchungen zu dem Ergebnis, daß der distale Bereich des Unterkiefers der Nachtschwalbe *(Caprimulgus europaeus)* — also das V-förmige Teil aus Symphyse und den vorderen Teilen der Unterkieferäste — in sich relativ starr sei und seine Form während der Aktionen des Unterkiefers kaum verändere. In Wirklichkeit ist aber unmittelbar caudal der Symphyse eine biegsame Zone im Bereich des Os dentale ausgebildet, so daß der Unterkiefer der Nachtschwalbe durch zwei Paar intramandibulare Artikulationsmöglichkeiten gegliedert ist (BÜHLER 1970, Abb. 7, 9, 27, 29). LUBOSCH kommt zu seiner Fehldarstellung der kinematischen Verhältnisse in der Symphysenregion des Unterkiefers, weil er vom alkoholkonservierten Präparat auf das lebende Tier schließt, ohne den Schluß nachträglich kritisch in Frage zu stellen und zu überprüfen.

2. Ebenfalls nach LUBOSCH (1929) soll beim Öffnen des Schnabels der Nachtschwalbe und dem damit verbundenen Absenken des Gesamtunterkiefers zusätzlich noch die distale Hälfte des Unterkiefers abgesenkt werden. In Wirklichkeit wird aber beim Absenken und Spreizen des Gesamtunterkiefers der vordere Bereich relativ zum Rest nicht zusätzlich noch weiter abgesenkt, sondern angehoben. Dabei drehen sich die Unterkieferastteile um ihre Längsachsen, und zwar in entgegengesetzten Richtungen:

* Der Begriff Funktion wird in dieser Abhandlung im Sinne von Funktionieren verwendet, also für die Arbeitsweise eines Organs oder Organteils, und nicht im Sinne von biologischer oder ökologischer Rolle.

Institut für Zoologie der Universität Stuttgart-Hohenheim, Bundesrepublik Deutschland

Von dem caudalen Teil des Unterkieferastes wird die nach oben gerichtete Fläche einwärts gekippt, von dem distalen Teil dagegen die nach unten gerichtete Kante. Bei dem caudalen Teil des Unterkieferastes entspricht die in Ruhe nach oben gerichtete Fläche einem Kreisausschnitt, bei dem distalen Teil die nach unten gerichtete Kante, so daß die besprochenen Drehungen um die Längsachse dazu führen, daß die Teile des Unterkiefers sich beim Aufreißen der Mundöffnung in einen kreisförmigen Ring einordnen können, wobei die extreme Verbreiterung der Schädelkapsel und die damit verbundene Lateralwärts-Verlagerung der Quadratknochen (an denen die Unterkieferäste artikulieren) weitere Voraussetzungen dafür sind, daß aus dem eckigen und engen Unterkiefer der Ruhestellung die kreisförmige Beutefangöffnung entsteht (BÜHLER 1970, Abb. 1, 2, 8, 24, 25, 26, 27). Also obwohl der distale Teil des Unterkiefers beim Öffnen des Schnabels in Wirklichkeit deutlich angehoben wird, kommt LUBOSCH zu dem Ergebnis, daß der distale Teil des Unterkiefers relativ zum Gesamtunterkiefer abgesenkt würde; und zwar kommt LUBOSCH offensichtlich zu dieser Ansicht, weil die Absenkung des vorderen Bereiches genau seiner Streptognathie-Theorie entspricht — also jener Hypothese aus der Säugetierkunde, die besagt, daß als Voraussetzung für die Entstehung des sekundären Kiefergelenks der Mammalia (also des Anlagerungsgelenks zwischen Dentale und Squamosum) der Unterkieferast der Säugetiervorfahren schon vorher in sich beweglich war. Die Übereinstimmung zwischen einer Lieblingstheorie und dem vermeintlich bei der Nachtschwalbe festgestellten Mechanismus war für LUBOSCH evident genug, um die gefundene Hypothese zu akzeptieren.

3. Nach FOURIE, der 1955 eine Dissertation über die Schädelmorphologie und Schädelbeweglichkeit einer Nachtschwalbenart *(Caprimulgus pectoralis)* publiziert hat, sollen die Caprimulgiden nur eine geringe oder gar keine Oberkieferbeweglichkeit haben, obwohl in Wirklichkeit bei diesen Vogelarten eine typische prokinetische Beweglichkeit des Oberschnabels ausgebildet ist (BÜHLER 1970, Abb. 3, 22, 23, 31), und zwar kommt FOURIE zu dem Fehlschluß, weil er annimmt, man könne aus der Form die Funktion ableiten. In Wirklichkeit kann man natürlich aus der Form nur eine Hypothese über die Funktion ableiten, was nichts anderes heißt, als daß man verpflichtet ist, im nachhinein die Tragfähigkeit der zunächst gemachten Annahme kritisch zu überprüfen.

4. Unklar sind die Verhältnisse der Oberkieferkinetik beim Strauß *(Struthio camelus)*. Bei allen Vögeln befindet sich unter dem Schädeldach in der Stirnregion zwischen den Augen ein knöchernes Interorbitalseptum. Bei den prokinetischen Vögeln, die den Oberschnabel als ganzes bewegen können, ist dieses Septum genau unter der Biegezone des Oberschnabels ausgespart. HOFER hat 1955 darauf hingewiesen, daß diese Aussparung, die sogenannte Fissura facio-cranialis, eine wichtige Voraussetzung für die Oberkieferbeweglichkeit darstellt. Beim Strauß jedoch fehlt solch eine Aussparung: Das Interorbitalseptum geht ohne Unterbrechung in das Nasalseptum über. BOCK hat deshalb 1963 diskutiert, daß beim Strauß die Biegezone des Oberschnabels vor dem Ende des medialen Septums ausgebildet sein müßte. Wenn man aber die Querschnittsform des Oberkieferskeletts anschaut, dann fällt auf, daß der Schnabelfirst genau in der Region vor dem Ende des medialen Septums gewölbt ist, während die Schnabelfirstspange im Bereich über dem Nasalseptum flach ist. Da eine gewölbte Knochenplatte sich aus mechanischen Gründen nicht oder nur schwer biegen läßt, muß eine andere Hypothese gesucht werden: Der Oberschnabelfirst läßt sich möglicherweise

nicht vor, sondern über dem Septum durchbiegen. Wenn aber das der Fall ist, dann darf der Schnabelfirst natürlich nicht mit dem Nasalseptum verwachsen sein, wie das z. B. bei den Waldschnepfen *(Scolopax)* der Fall ist. Bei einem präparierten Straußenschädel, bei dem der Oberschnabel in leicht angehobener Stellung fixiert ist, läßt sich tatsächlich feststellen, daß zwischen Septum und Oberkiefer ein Spalt ausgebildet ist. Dem entsprechen auch ein lockeres Bindegewebe zwischen Nasalseptum und Schnabelfirst, das histologisch nachgewiesen werden konnte, und die passive Beweglichkeit des Oberkiefers, die an frischtoten Köpfen aus Südwestafrika untersucht werden konnte, wobei sich ergab, daß tatsächlich über dem Nasalseptum eine Biegezone im knöchernen Schnabelfirst ausgebildet ist (Bühler & Frey-Lühl). Durch Untersuchung von Schliffen aus dieser Region mit dem Lichtmikroskop und einem Spezialröntgengerät ergab sich weiterhin, daß der Schabelfirst in der Biegezone aus zwei Knochenlamellen und einer zwischengeschalteten Bindegewebsschicht aufgebaut ist — also entsprechend dem Prinzip einer Sperrholzplatte oder der mehrschichtigen Blattfederung eines Eisenbahnwaggons.

Dieses Beispiel des Nachweises einer besonderen Biegestruktur im Straußenoberschnabel zeigt exemplarisch, was mit den einzelnen Schritten in dem Schema der Abb. 1 gemeint ist, und wie sich durch das Prinzip der hintereinandergeschalteten Hypothesenüberprüfungen die Unterlassungen der ersten drei Beispiele vermeiden lassen: Ausgehend von einer in der Literatur vorgegebenen Fragestellung führte der Weg über die Formulierung der Hypothese zu deren empirischen Überprüfung; im Falle der Widerlegung der Hypothese dann zur Ersetzung durch eine Alternativhypothese, die allen bisherigen empirischen Befunden genügen muß, und die dann weiteren empirischen Überprüfungen zu unterwerfen ist. Im vorliegenden Beispiel hielt die Alternative diesen Überprüfungen stand — die Hypothese bewährte sich im Sinne von Popper (1976). Angeregt durch dieses Ergebnis kam es dann zur Suche nach ergänzenden Hypothesen (vgl. Hypothese vom Sperrholzprinzip in dickeren biegsamen Knochenplatten und in Abb. 1 den direkten Pfeil von der „Hypothese mit Anspruch auf Allgemeingültigkeit“ zur „problemorientierten Untersuchung der Objekte“).

Konsequenzen und Zusammenfassung

Erstens: Die an Hand der Beispiele demonstrierten methodologischen Forderungen entsprechen im Prinzip dem Vorgehen vieler Funktionsmorphologen, die sie bewußt oder unbewußt schon bisher in richtiger Weise befolgt haben. Da sie aber andererseits oft vernachlässigt oder gar ignoriert werden, wurde versucht, die wesentlichen methodischen Schritte der funktionsmorphologischen Vorgehensweise herauszuarbeiten: Zwei grundsätzlich verschiedenartige Schritte sind unabdingbar. Erstens die Findung von funktionsmorphologischen Hypothesen und zweitens deren empirische Überprüfung. Für die Findung der Hypothesen gibt es zwar grundsätzlich keine zwingende Vorschrift (vgl. Gutmann et al. 1975), aber für den funktionsmorphologischen Bereich hat sich die intensive Untersuchung der Objekte — also der morphologischen Details, der passiven Beweglichkeit am frischtoten Objekt und der Beobachtung freilebender oder in Gefangenschaft gehaltener Individuen etc. als Grundlage für die Hypothesenprovokation besonders bewährt. Für das Auffinden von Konstruktionen mit ungewohnten Funktionsweisen ist in der Regel auch ein fundierter Überblick über das Wissen aus den Bereichen der vergleichenden Anatomie, der ökologischen Ethologie und

der Biomechanik notwendig. Deshalb werden durch funktionsmorphologische Erstlingsarbeiten, wenn sie nicht im Rahmen einer intensiven Zusammenarbeit mit erfahrenen Funktionsmorphologen durchgeführt werden (trotz des meist beachtlichen Umfangs solcher oft als Dissertationen vorgelegten Arbeiten), häufig nicht die wesentlichen Phänomene erfaßt, die im Rahmen der Bearbeitung eigentlich erfaßt werden sollten.

Zweitens: Die Wahrscheinlichkeit, daß für eine funktionsmorphologische Fragestellung zunächst eine falsche Hypothese gefunden wird, ist zwar ebenfalls recht groß. Aber das Finden einer falschen Hypothese ist nicht von so negativer Bedeutung wie das Übersehen eines wesentlichen Phänomens, weil falsche Hypothesen bei einer nachgeschalteten Hypotheseüberprüfung sich auswechseln lassen, während übersehene Funktionskomplexe aus dem Gesichtsfeld des Untersuchers geraten.

Drittens: Die Überprüfung einer Hypothese kann nur durch das konsequente Bemühen erfolgen, die Hypothese zu widerlegen, solange sinnvolle und empirisch überprüfbare Einwände gegen die Hypothese erkennbar sind (vgl. Popper 1976). Dabei sind die Einwände gegen eine Hypothese als überprüfbare Vorhersagen zu formulieren (in

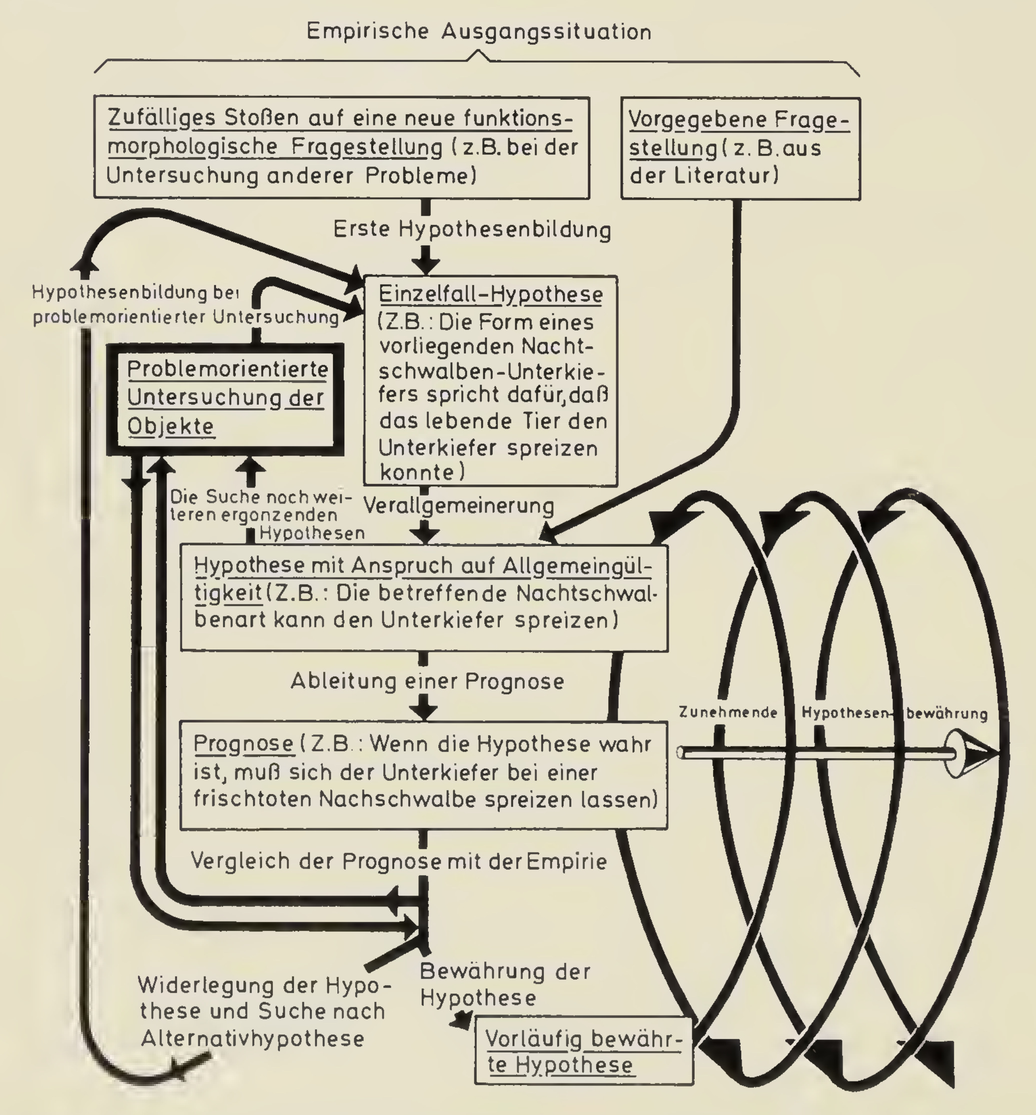


Abb. 1. Schema der Bearbeitung einer funktionsmorphologischen Frage (als Beispiel ein Detail der Kiefermechanik einer Nachtschwalbe). Die Spirale symbolisiert das sich fortsetzende Wechselspiel zwischen Prognosenableitung und Prognosenüberprüfung, durch das nacheinander alle vorliegenden Einwände gegen eine Hypothese empirisch zu überprüfen sind; wenn eine Überprüfung negativ ausfällt, ist die Hypothese zu verwerfen und durch eine Alternative zu ersetzen, die den bisherigen empirischen Befunden genügen muß.

Abb. 1 als „Prognose" gekennzeichnet), an Hand derer sich dann empirisch überprüfen läßt, ob die Hypothese falsch ist oder ob sie sich bewährt. Durch dieses sich wiederholende Wechselspiel zwischen intuitiver Hypothesenfindung, Ableitung von Prognosen und der empirischen Überprüfung (das in Abb. 1 als Spirale zur „zunehmenden Hypothesenbewährung" führt) ergibt sich mehr oder weniger zwangsläufig auch die Auswahl der morphologischen Merkmale, die bei einer Bearbeitung besonders intensiv untersucht und auch in der graphischen Darstellung herausgehoben werden müssen. Wichtig ist es, bei der Überprüfung einer Hypothese möglichst präzise Verfahren zu finden und anzuwenden (also Prüfverfahren, die dann, wenn eine Hypothese falsch ist, auch die Hypothese zu Fall bringen). Das Finden solcher Prüfverfahren ist zwar grundsätzlich eine Frage der Intuition, aber z. B. speziell für den funktionsmorphologischen Bereich des Nahrungsaufnahmeapparates hat es sich bisher schon bewährt, Hypothesen durch gezielte Untersuchung bestimmter morphologischer Details (wie z. B. des Verlaufs und der Mächtigkeit beteiligter Muskeln) in Frage zu stellen, weiterhin durch Untersuchung des Einflusses von Konservierungsmethoden auf Statik und Kinematik, durch gezielte Untersuchung der Bewegungsmechanik am frischtoten oder lebenden Tier; auch durch den Einsatz von Meßtechniken zur quantitativen Erfassung von Kinematik, Elastizität, Belastbarkeit, Proportionen und Substanzmassen; in manchen Fällen durch licht- und elektronenmikroskopische Untersuchungen des inneren Feinbaus, der für Statik und Kinematik eines Systems von Bedeutung sein kann; weiterhin durch entsprechende Verhaltensuntersuchungen (Beobachtungen, Kinemato- und Röntgenkinematographie, Zeitdehnungstechniken, Elektromyographie, Videotechniken); schließlich durch Methoden der angewandten Mathematik, der graphischen und numerischen Mechanik, durch spannungsoptische Untersuchungen und durch den Bau von mechanischen Vergleichsmodellen usw. usw. — wobei, wenn möglich, eine nicht zu kleine Anzahl von Individuen und verschiedener Altersstufen und natürlich auch alle (!) entsprechenden Befunde in der Literatur in die Prüfverfahren einzubeziehen sind.

Grundsätzlich ist es in keinem Falle akzeptabel, die Prüfung einer Hypothese auf die Suche und das Zusammentragen von positiven Argumenten zu beschränken, die eine Hypothese unterstützen, da schon eine einzige empirische Widerlegung ausreicht, um eine Hypothese trotz einer Vielzahl von positiven Argumenten zu Fall zu bringen (vgl. bei Popper die Asymmetrie zwischen Falsifikation und Verifikation). Deshalb sollte eine funktionsmorphologische Hypothese nur dann im Rahmen von Publikationen dargestellt werden, wenn sich der Autor schon intensiv um die Findung und empirische Überprüfung von Gegenargumenten bemüht hat.

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Studies of Functional Anatomy in Birds Utilising Museum Specimens

P. J. K. Burton

Museum specimens were the basic material used in the numerous 19th century anatomical studies which laid the foundation for modern functional morphology. Although techniques and objectives have changed, museum specimens still have their part to play. The purpose of this paper is to examine their role at the present day, and to suggest possible directions of future development.

We should perhaps start by considering the specimens themselves. Where anatomical work is concerned, it is almost taken for granted that "specimens" refers to birds preserved whole in fluid, or to skeletons. It should not be forgotten, however, that the traditional skin specimens which form the bulk of most collections can furnish useful data. This will mainly consist of more detailed measurements of legs, wings and bill than are usually required for species level taxonomic work. Occasionally the skull may be of use when no osteological specimen is available, and can be either exposed completely, or revealed by soft X-ray. Unfortunately, the common practice among skinners of cutting out the palate and much of the occipital region greatly reduces the usefulness of many specimens.

Fluid preserved specimens are usually stored in ethyl alcohol or iso-propyl alcohol. Their condition will depend upon the method of fixation used initially, and upon the standard of subsequent storage. Both of these vary widely. Fixation was often poor in many older specimens, and I suspect many are simply a surplus which the collector had no time to skin, and eventually crammed into an insufficient supply of spirit at the end of the day, after several hours decomposition and dessication. Such specimens have brittle soft tissues, and often a dried and distorted tongue. Occasionally a mass of dipterous larvae is found where a muscle should be. (These at least are well preserved, having been alive until the time of fixation!) In fairness, however, many old specimens are in excellent condition, and I have obtained useful information from a specimen of *Creadion carunculatus* believed to have been collected 200 years ago (Burton, 1969, 1974 a), and produced reasonable histological sections from a specimen of *Heteralocha* over 100 years old. Specimens collected by the British Museum (Natural History) in recent years are fixed with 8 to 10 % formaldehyde solution, or a formaline based fixative; the use of glycerine apparently promotes pliability. Formaline fixed specimens often have the slight disadvantage of rather colourless muscles; this can be overcome by the use of iodine solution (Bock & Shear, 1972). Fixation is performed as soon after death as possible, normally within half an hour. All but the smallest birds are injected as well as immersed, and weights at death are recorded—a vital piece of anatomical information which has all too often been omitted in the past.

The main danger during storage is that specimens may dry out due to evaporation of spirit. Although modern containers greatly reduce this danger as compared with old style museum jars, the only real safeguard is constant vigilance, and a programme of regular retopping. Unfortunately, over the years, periods occur during which the curators of the time have little interest in spirit specimens, and it is at these times when dete-

Subdepartment of Ornithology, British Museum (Natural History), Tring, Herts. HP23 6AP, England, UK

rioration has occurred. We know from manuscript remarks by William Clift, a nineteenth century curator of the Hunterian collection, that such a period of neglect occurred at the British Museum during the late eighteenth and early nineteenth centuries, and it would be unrealistic to suppose it has not happened more than once since.

Skeletons are more laborious to prepare, but once this has been done, are the easiest to maintain of the various kinds of museum specimens. The main danger is that during use for comparative study, parts of different specimens may become muddled. The only effective precaution is to mark all parts of a skeleton with its registration number—a laborious and time consuming process.

Let us now consider the types of information which a functional anatomist may hope to obtain from these specimens. Measurements and descriptions of form based on skeletons should be relatively error free, providing normal precautions are taken to ensure consistency. Possible pitfalls may occur with the skull, which may have dried out with the upper jaw and palate in various positions. If basipterygoid processes are present, they provide an indication of the state of retraction or protraction of the specimen. If kinesis itself is being studied, the upper jaw and palate may be rendered mobile by soaking. Various devices have been constructed for measuring kinesis, but I am personally rather cautious about this technique, since the state of the specimen (especially its age) may considerably affect results. I would urge the use of either fresh material, or skeletons of the same age and identical method of preparation, for this purpose (see Goodman & Fisher, 1962).

Regarding the dissection of spirit specimens, I am most conversant with problems affecting myological work. These arise from the great variations in apparent bulk, position and fibre orientation which may be produced simply by chance events during preparation of the specimen. When these problems are considered in relation to the depth of information needed to fully understand the functioning of a muscle (Bock, 1974), it might well be thought that no useful conclusions could be obtained at all from preserved specimens. Nevertheless, study of a range of species eventually reveals consistent differences requiring explanation, and I shall consider the methodology involved in the concluding part of this review. Before leaving this topic, I would like for a moment to comment on the practice of weighting muscles or other tissues and organs to assess their bulk. This was done by Goodman & Fisher (1962) for a range of Anatidae. For reasons which are thoroughly explained in Bock's (1974) review, I believe these weights to be of limited value on their own. Nevertheless, they could perhaps be of use in the future, but some practical problems will have to be overcome. These concern weight changes in museum specimens during fixation and preservation. Norris & Williamson (1955) considered that hearts preserved in 10 % formalin did not differ significantly in weight from fresh hearts, but a study of my own (Burton, 1977) suggested weight loss in alcoholic specimens. Skeleton specimens must also vary in the extent of weight loss. For these reasons, specimens used to provide weight data should be closely matched for method of preparation and storage; if this can be done, there is a relatively untapped potential here which may eventually produce much valuable information. There are probably other areas of investigation which could utilise museum specimens but have as yet been little pursued. Histology is probably one of these; although museum specimens have their limitations for this purpose, they are usually adequate for at least simple comparisons of tissue structure. Even more neglected are the many spec-

imens of embryos which exist in most spirit collections of birds. Many of these probably represent the technical failures of egg collectors, but it seems unfortunate that they are so little used. This is perhaps because their stages of development are so variable that inter species comparisons would be difficult, or because embryologists do not know they exist, or because they simply do not require them. However, I am reluctant to believe they cannot be usefully employed in some way!

From the foregoing remarks, it will be evident that museum specimens have their limitations. The type of study in which they will play only a supporting role is well exemplified by the work of Zweers (1974) and Zweers et al. (1977) on the feeding apparatus of the Mallard *(Anas platyrhynchos)*. Techniques used in such a thorough analysis may include in vivo experimental studies of muscle or nerve-muscle preparations, refined histological techniques and ciné-photography of behaviour. Studies of this depth are vital if the functional significance of morphological features is ever to be thoroughly understood. However, it is equally essential to view them in a wide perspective throughout a range of species. Since it is scarcely feasible to treat all these species with the same thoroughness, recourse must be had to museum collections.

The type of study for which museum specimens are ideally suited therefore, is a wide ranging survey, taking in as many species as possible. Theoretically, the more species examined in such a survey, the more accurate are likely to be its conclusions. Its conclusions will largely be based on the distribution of structural features among the species examined, and particularly on associations between such features, or between structure and behaviour. However, there are obviously practical limits set by the time and stamina of the investigator, and there is a danger of attempting too wide a coverage, and achieving only a superficial level of understanding. There are two possible remedies for this. The most obvious, of course, is to limit coverage to a fairly small number of species, so that all can be studied in some detail. Examples of papers in the last two decades following this method are Zusi's (1962) study of the Black Skimmer *(Rynchops nigra)* and three other Lariform birds, or Goodman & Fisher's (1962) study of a number of Anatidae. An alternative is to study one or a few species in special detail, and proceed from this to a simpler, more stereotyped survey of a wider range. This has been the approach adopted in a number of papers by Bock, e.g. of secondary articulation of the avian mandible (Bock, 1960 a) or the palatine process of the premaxilla in the Passeres, and I have tended to favour it myself, as in a study of the Charadrii (Burton, 1974 b) or a more recent one of the Coraciiformes and Piciformes (Burton, in prep.). The study of the stapes by Feduccia (1975), though limited to one structure, is essentially of this type. Nevertheless, studies of this wider type have not been pursued by many recent workers in avian functional anatomy, although several primarily systematic studies have drawn on a large array of species, e.g. Ames (1971), van den Berge (1970), Strauch (1976).

There are pitfalls in both approaches. The first suffers from the limited number of species investigated, but in the second, the dangers are more subtle. They arise from the fact that since not every detail can be checked in the wider stage of the survey, some selection has to be exercised. There is thus a possibility of subjective bias, which can be guarded against only by careful thought and constant checking. In practice, feedback occurs between detailed dissection of selected species, and checking of simple points in a range of others. Thus, in my study of the feeding apparatus in the Chara-

drii, what started as a simple check of the relative development of components of M. pterygoideus revealed a major dichotomy within the group, based on the pathway followed by N. pterygoideus. This had gone unnoticed in the initial dissections of five representative species, although both types of structure were represented. Further checks on additional species eventually revealed the existence of intermediate conditions in *Pluvianus* and *Peltohyas.*

Studies utilising one or a few species only are of value when "in depth" investigation is impossible for practical reasons, and unusual features are present for which a wider survey would only marginally improve understanding. Such studies are understandably attractive to investigators, since they are usually short but interesting; they may even serve a useful psychological role by relieving the tedium of a long term project! Casting an eye over the literature of recent years, I see I have quite often fallen prey to this temptation, with e.g. papers on *Eurynorhynchus* (1971), *Anarhynchus* (1972), *Heteralocha* (1974) and *Procnias alba* (1976). Papers by others falling into this category include, e.g. Bock (1961) on *Perissoreus* and (1969) on *Pedionomus,* or Zusi & Storer (1969) on *Podilymbus.* Such investigations have a useful contribution to make, since the extreme features shown by most of these birds may highlight factors which have influenced the evolution of less specialised relatives.

A final question arises from the foregoing review; can the world's museum collections supply the specimens needed for such studies? The answer is a cautious and qualified affirmative. A recent survey of the anatomical collections of the British Museum (Natural History) by Blandamer & Burton (in press) shows that all families but one (Atrichornithidae) are represented by at least a single specimen, while coverage of genera is 61 % and of species 40 %. However, only a few other collections in the world are as large, and even the British Museum (Natural History) collection leaves many serious gaps. Curators in charge of anatomical collections of birds will no doubt be concerned to fill these gaps, but it is not always at once obvious which deficiencies are the obvious ones. Personal involvement in research on avian anatomy is vital, for only in this way can important desiderata be identified, and priorities determined. Having decided these priorities, there may still be difficulties, for the world has changed since the heyday of collecting in the nineteenth century. Many species are too rare to sustain even moderate pressure on their populations, while collecting activities in many countries are unpopular, for reasons which are sometimes as much political as they are conservational. To conclude, then, I would urge closer cooperation between ornithologists in charge of such collections, to devise a common policy aimed at providing a comprehensive stock of material for future anatomical studies.

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Experimental Functional Analysis and Formulation of Causal Models

GART ZWEERS

Introduction

Waterfowl show a wide radiation of feeding methods on one broad unifying pattern. Therefore, their feeding systems provide an extremely good opportunity to undertake comparative studies in order to clarify the shaping of that system. Prior to the selection of structural parameters for comparison, the complete functional and ecological morphology of the system should be known. A clear research strategy arising from a particularly formulated methodology is a first requirement for such an approach. Hence, a short compilation of hypotheses involved is given (cf. ZWEERS & KOOLOOS, 1978). Newly found structures in the biocybernetics of the system are listed first and then the biomechanics (cf. movements and electric activity) are analyzed in order to formulate causal models for pecking and straining. The progress of this research along the methodological pathway is indicated by showing the measurement of quantified role-fulfilment as a basis for a first approach optimization and systemization.

Methodological survey and research strategy

Question

Functional (and ecological), developmental and evolutionary morphologists basically answer the following question: "Why is a system built the way it is, and why not different?" Asking "why" involves two well known aspects: (1) as a result of which evolutionary and developmental processes arrived the system at its present state, and (2) whatfor and how does the system work? Asking "why not" implies that the system could be different. Seen from an holistic or system analytic point of view it is stated that each system is incorporated in larger hierarchically higher systems. Hence, the system must fit in the higher ones. So there must be hypothesized systemic conditions that limit and design the realization of a system. That is not saying that a feed-back to the genotype must be included in this hypothesis.

System on three time levels

A biological system exists along three time levels: The evolutionary, the developmental, and the momentary time level. This report focusses on the third time level, neglecting for this moment both other time levels, and hence tries to answer the "why not different"-question only on the momentary time level.

Causal models

The limits of a system are defined by the biological roles or functions studied. The infinite totality of structural and action parameters of a system are abstracted by selection of characteristic parameters. These parameters should be put together in a causal model to clarify the particular investigated role. The "causal" refers to the structure of the model, which is: If structure A shows action 1, then this will result in action 2 of

Dept. Morphology, Zoological Laboratory, Leiden, The Netherlands

structure B to fulfil the particular role. As soon as the causal model is formulated, three "follow up" terms are used: (1) Construction = the set of selected structural parameters used in the causal model, and (2) Operation = the same for the actional parameters, and (3) Rolefulfilment = the set of role parameters selected to be clarified in the causal model.

The functioning feeding system of birds can be formulated as chains of causal models. Finally these chains will tend to form ring-like networks. The ring can be subdivided roughly in 7 steps: Relative muscle forces to (1) movements of sustaining elements to (2) movements of surface structures to (3) movements of food to (4) taste and touch signals to (5) exteroceptive brain activity to (6) $\alpha-\gamma$ motor neuron activity to (7) relative muscle forces. The first four steps are called the biomechanics, the last three steps are called the biocybernetics of the system (cf. a more detailed picture in Fig. 1).

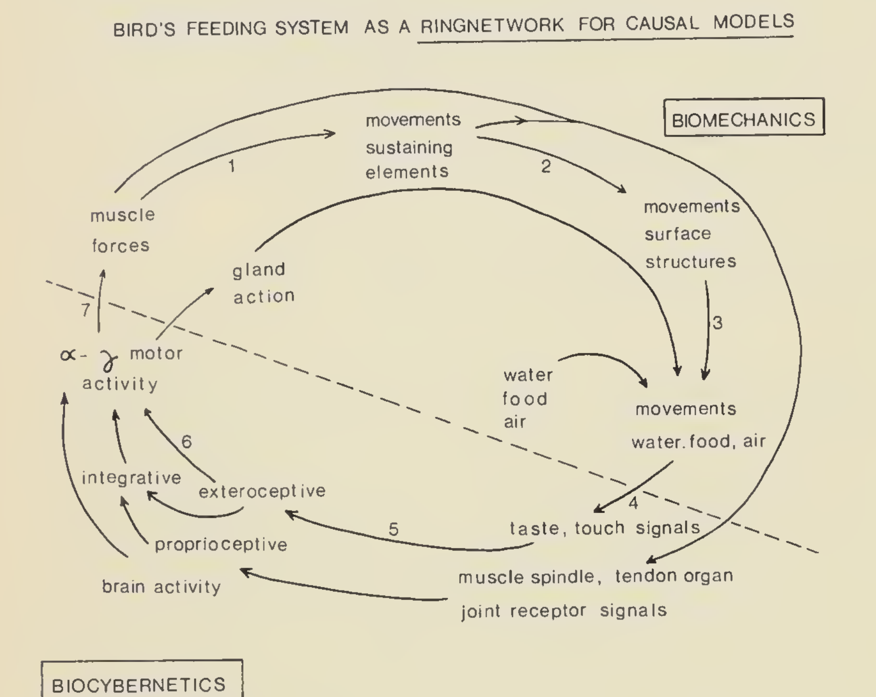


FIGURE 1. A bird's feeding system as a ring network for causal models (explanation in the text).

Optimizing and systemizing

It is stated from the foregoing that it must be ascertained if, and if so which, alternatives for a system are realizable. Therefore, the causal models should be falsified and after that transposed into the original one or alternatives. The following question is formulated to arrive at falsifying: How should construction and operation be realized for a particular quantitative rolefulfilment, if all other rolefulfilments were absent? And for the reversed transposition: If such a realization is formulated for all rolefulfilments of a system, how are these realizations transposable into one system? Therefore, three hypotheses are used: (1) the actual system is the result of some balance between two opposing drives: a shaping and a deformating one, and (2) the shaping drive is presented by optimization (of the causal models for all of its different rolefulfilments), and (3) the deformating drive is presented by systemization (of the optimized causal models). Game theory is advantageous for tracing rules for systemization. The different rolefulfilments are to be seen as opponents playing a game with reference to structural and action parameters. The game has one basic rule: If one of the original quantitative rolefulfilments "gets hurt" a further transposition of parameters is to be stopped.

Research strategy

The research strategy is summarized as follows: (1) selection of main roles of the system, (2) structure, action and role analyses, (3) causal model formulation as an operating construction fulfilling a particular role, (4) optimizing causal models for the main rolefulfilments in quantitative terms, (5) systemizing the optimized causal models by gaming, and (6) experimental or natural test.

Food discrimination, straining and pecking

First the biological roles are selected. If a trained mallard is offered a mixture of equal weights in water of rounded seeds with increasing diameters (mow seeds ~ 0.7 mm, millet ~ 1.0 mm, round seeds ~ 1.5 mm, spherical seeds ~ 2.0 mm) it first strains millet, then 1.5 mm seeds, while mow seeds are thrown out at the mouth corners, then mow seeds, then 2.0 mm seeds. This order of preferences leads to two conclusions. The mallard is able to "set" his straining feeding system for a particular diameter of food once the seeds are selected priorily on their taste. The taste detection must take place far rostrally in the beak, and the diameter detection by touch must take place between or even in front of the beak tips. Similar conclusions are drawn from the "pea-clay ball" experiments of Zweers & Wouterlood (1973). It is stated that during pecking, the third role on which is focussed, discrimination is similar but has a different tolerance and effectiveness.

Biocybernetics

The structure analyses resulted so far in a confirmation with the general picture of senses and central connections as known from the literature. However, a series of new findings is made that completed the picture and made the omissions clear.

The highly organized bill tip organ (cf. Fig. 2 for numbers, 15) for touch sensation is described by Berkhoudt (1976). The complicated maxillary cushion (9) in the upper bill tip has a field of huge corpuscles of Herbst and has a group of taste buds around the monostomatic openings of the glandulae maxillaris (16) (Berkhoudt, 1977). Network fields of both types of avian touch corpuscles lie in the tongue (8), upper and lower beak (18) and underneath the lamellae (7, 19). A second newly found taste area is situated far rostrally in the lower beak (9), third and fourth area is found dorsal to the lingual cushion in the upper beak (11). These taste fields lie along the food track at places where the food is relatively at rest.

The subdivision of the ganglion semilunare (20) and the nucleus principalis nervi trigemini (30) into 4 parts was found by Dubbeldam (1975, 1978). The latter has a maxillary, a mandibular, an ophthalmic and an unexpected glossopharyngeal projection area. This suggests a bringing together in a "touch-processing" information running via quite different nerves (V and IX) and originating periferally in areas which cooperate closely in their biomechanics. A similar feature is found for a "taste-processing" area in the nucleus principalis nervi facialis (35, sVIId in Dubbeldam, 1977) where taste information could arrive via the nervus facialis and nervus glossopharyngeus. Final projection of the afferent trigeminal nerves is also found in the nucleus oralis (31), n. interpolaris (32), n. caudalis (33) and the substantia gelatinosa (34). Ascending projection is found so far only from the n. caudalis into the thalamus (27) (p. c. Arends) and via the

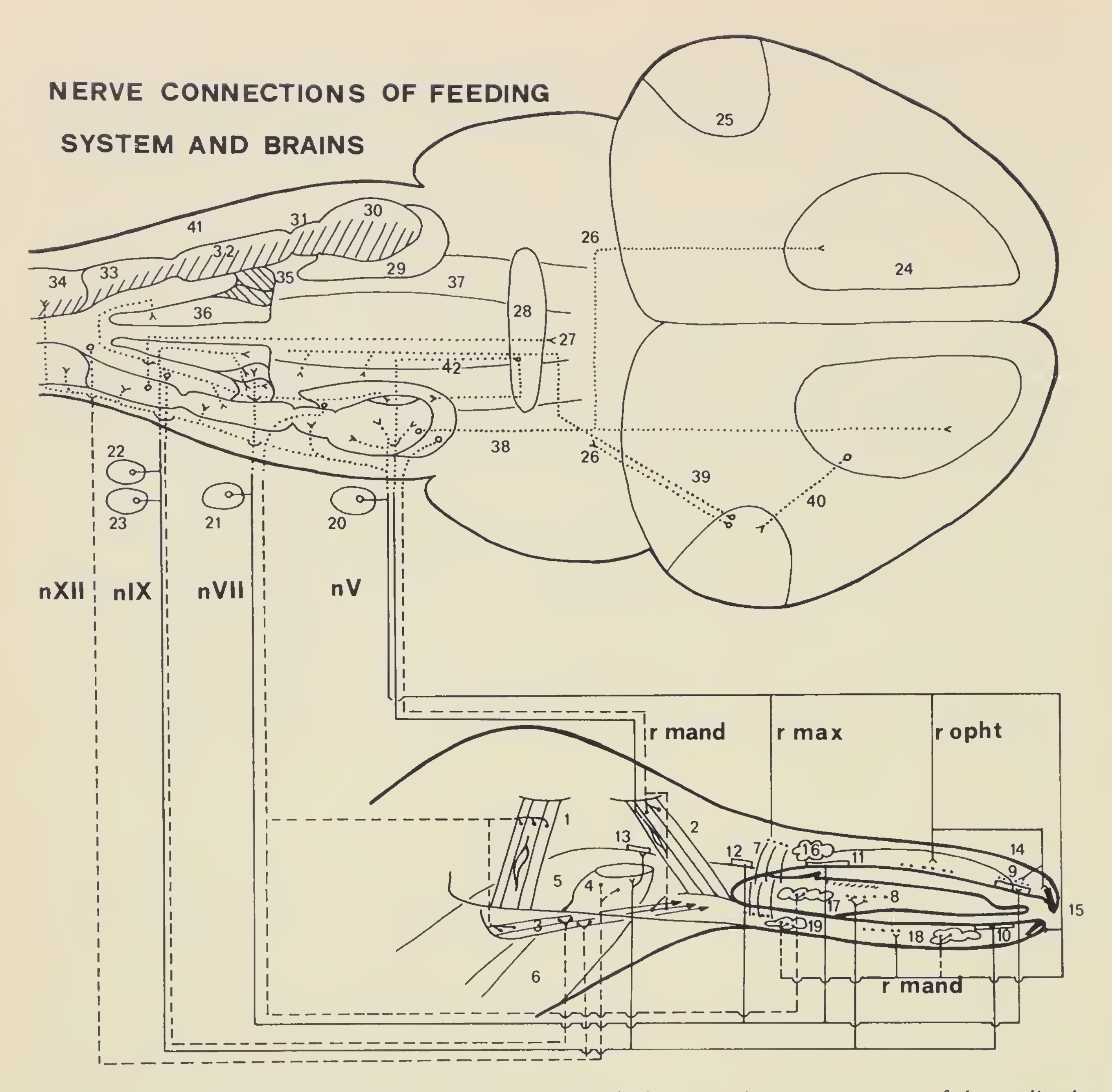


FIGURE 2. Nerve connections of the feeding system with the central nervous system of the mallard (explanation in the text).

well known huge tractus quinto frontalis (38) into the nucleus basalis (24, DUBBELDAM, MS.). No other ascending projections are found at yet. Feed back on the motor nuclei is to be traced.

Biomechanics

The mechanical part of the feeding system consists of three subsystems: The muscle-bone-ligament, the surface structure, and the glandular subsystem.

The muscle bone system

This part is composed of a beak and a tongue system. Both systems must be described very accurately starting with the sustaining elements, with emphasis on joint structures and on rigidity or elasticity of bones and cartilage. This serves to enable the abstraction into a line diagram in which bars, their freedom of movement and flexibil-

ity are shown. Next the ligaments are described and abstracted as unstretchable but foldable lines connecting points on the bars, thus restricting the possibilities of the movements. Finally the muscles are described in very great detail to enable their abstraction as working lines. These lines generally run between origin and insertion, they indicate the most probable lines along which forces can be developed on the basis of position of muscle fibers and aponeuroses. These working lines decide which movements can be carried out. Once the systems are abstracted in this way, the actual change of position of the sustaining elements must be traced during the studied roles: Pecking and straining. This is done by X-raying and filming, and frame by frame analysis. Simultaneously electromyograms must be made of all the muscles involved to learn which force generators are active to perform the movements. Once the working-line diagram is available and transposed into a series of diagrams in which the change of positions of bars and lines is indicated according the movement analysis of the selected role, a causal model can be formulated. Therefore the emg of each muscle is to be transposed into a vector. The direction of the vector is known from the position of the working lines. The relative size of the vector is calculated by multiplication of the relative physiological cross-section of the muscle and relative size of the integrated emg. These values are drawn in the series of working line diagrams. The question to be answered for the movements in the beak system in the first causal model in the "causality ring" is: Can the vector diagram in the stage prior to the present one explain the position of the beak tips in the present stage? (cf. ZWEERS, 1974 for straining). The same question holds for the rostrocaudal movements of tongue and glottis, and the dorsoventral movements of lingual tip, lingual bulges and lingual cushion (cf. ZWEERS et al., 1977, for straining, and ZWEERS & KOOLOOS, 1978, for pecking).

The surface structure system — Straining

The third model in the "causality ring" clarifies the actual change of the position of food as a result of movements of the surfaces structures. The suctioning action of food and water can be compared with that of a suction pressure pump. Therefore the system is looked upon as a cilinder (beak) with an inflow opening (beak tips) and outflow opening (lamellar area) in which two pistons move which simultaneously act as valves (lingual bulges and lingual cushion). The filtering action is described as a film transporting system. Seeds are strained by the juxtapositioned upper and lower beak lamellae. Lower beak lamellae move the seeds dorsally into the longitudinal maxillar groove. The lingual scrapers transport them caudally into the pharynx between the lingual cushion and glottis, where they are collected. The swallowing is done by forcing the bolus over the glottis into the esophagus. Transporting down into the esophagus by peristaltics takes place after a second collectioning phase far rostral in the esophagus (cf. ZWEERS et al., 1977).

Pecking

The causal model for pecking is subdivided in the following phases: Grasping, stationing, throwing (and shot), transporting, collecting I, swallowing, collecting II, peristaltics. The last four phases are similar to those for straining. Straining lacks the grasp, the stationing and the throw plus shot. Pecked peas are stationed by lingual tip move-

ments which are similar to those of pecking pigeons. The lingual tip runs almost vertical rostralwards, thus pushing the pea between the closing beak tips, then the tip is pushed underneath the pea while the head moves backward and the beak starts to open. The pea is shot caudally by the push of the flexible rostrally running lingual tip at the moment the highest point moves underneath the pea and just prior to the opening of the beak. Simultaneously the head moves forward again and the tongue caudally. The combination of shot and fast rostral movement of the head results in a pea thrown caudal into the beak, even caudal relative to the tongue although the tongue is moving caudally (cf. Zweers & Kooloos, 1978).

Quantified rolefulfilment

Tolerance and effectivity

The last section showed clearly that one structure has two different actions to serve two different roles. Before any further comparison is done the quantitative rolefulfilment must be measured.

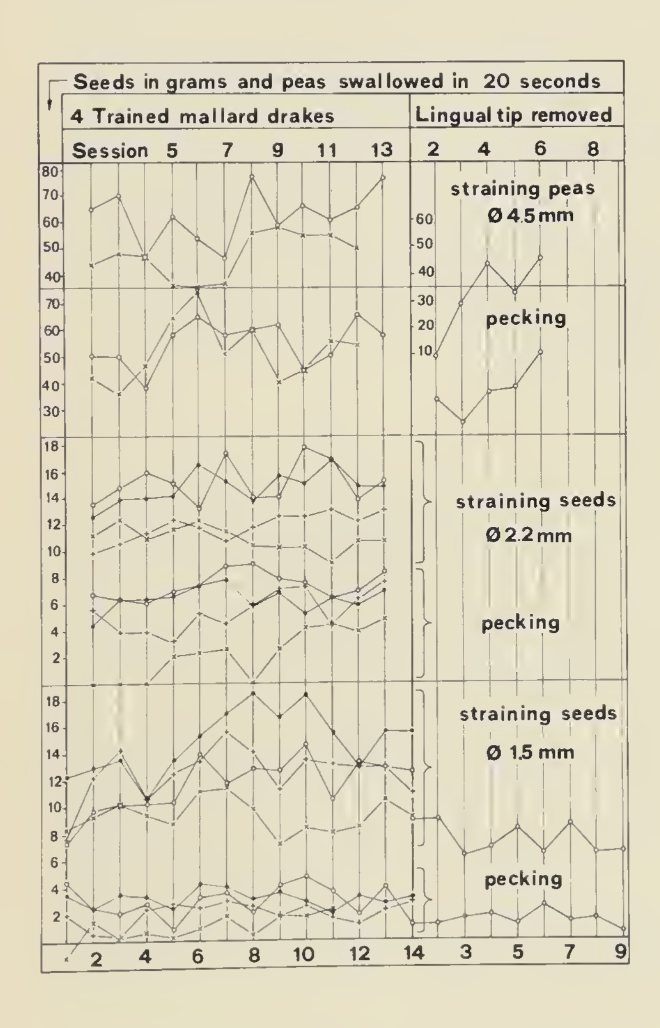


Figure 3. Seeds and peas swallowed in 20 seconds by straining or pecking (explanation in the text).

Tolerance is defined as the range of diameters of food particles (from peas to mow seeds in 6 steps) that a mallard is able to consume. Some individuals try vigorously to swallow peas but stay unable to do so, similarly some individuals pump water with mow seeds again and again, but stay unable to strain them. Thus quantification must be carried out on an individual basis. Effectivity is defined as the amount of food ingested per time unit. For pecking and straining peas the effectivity is found equally effective. The smaller the diameter of the seeds the more effective is the straining (cf. Fig. 3).

Optimization and systemization

Pea consuming has been used for a first approach optimization. Pea straining is optimized, that is to say made faster, by (1) increase of the frequency of the movements, and (2) increase of the pumping volume per cycle, etc. Further splitting of the second change results in (1) lengthening and widening of the mouth, (2) stiffening of the lingual tip to arrive at better guidance of the waterstream, etc. Pea pecking can be made faster by (1) increase of the frequency of the movement cycles, and (2) shortening of the food track, etc. Focussing on the second aspect teaches a further splitting by (1) shortening of the beak and the tongue, (2) straightening of the food track, (3) removal of obstacles such as lingual ears, lingual cushion, maxillary teeth, etc.

From the foregoing we arrive at the following conclusions:

(1) Since increase of frequency optimizes both roles, either the optimization hypothesis is wrong or there is interference with other roles such as discrimination. Hence the biocybernetical models are now a first consideration.

(2) Since increase of beak length optimizes straining and decrease optimizes pecking it is clear that some compromise is worked out. The way they interfere is traceable by describing rules according which these models are systemized (i.c. made one system).

(3) Since the elastic lingual tip and bulges are decisive for pecking and the lingual cushion for straining, it is clear that sometimes no compromise can be made. If any is desired from systemizing our optimized models, a system must be rearranged in its totality so that totally different alternatives may be expected.

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Ökomorphologische Freiland- und Laboratoriumsuntersuchungen

Bernd Leisler

Einleitung

Zentrales Thema in der Ökomorphologie ist die Frage, wie einzelne Strukturen oder Funktionskomplexe taxonomischer Einheiten (Art, Gattung), ökologischer Einheiten (Gilden, Communities) oder konvergenter Organismen (ökologische Vertreter) zur Fitness des Organismus bzw. der Organismen beitragen. Durch die Arbeiten von Bock (1977) und Peters et al. (1971) besitzen wir neuerdings ein gutes theoretisches Konzept der Ökomorphologie mit durchdachter Begriffsdarlegung und Verfahrensregeln. Die einzelnen Schritte der Untersuchung einer Anpassung lassen sich durch die Fragen: was (Form), wie (Funktionieren, Konstruktion) und wozu („Fungieren", biologische Rolle) charakterisieren.

Wenn man davon ausgeht, daß bei der Untersuchung einer Anpassung die Konstruktionsanalyse die zentrale Stelle einnimmt und daß ein Schluß von der biologischen Rolle einer Struktur auf ihre Konstruktion nicht möglich ist (Peters et al. 1971), ist klar, daß nur eine Kombination von Laboratoriums- und Freilandarbeit zum Ziel führen kann.

Die integrierte Untersuchung

Von Bock (1977) gibt es einige Vorschläge, wie solche kombinierten Studien gemacht werden sollten. Entscheidend ist, daß es während der gesamten Studie zu einer ständigen Rückkoppelung zwischen Laboratoriums- und Freilandarbeit kommt. Bei der Feststellung der biologischen Rolle eines Merkmales ergeben sich Schwierigkeiten aus der Kompromißnatur fast aller Konstruktionsteile des Organismus und aus ihrer funktionellen Interdependenz. Eine breite Kenntnis der gesamten Naturgeschichte der untersuchten Art(en) ist daher nötig. Bei einer zuwenig breit angelegten Studie ist die Gefahr groß, wesentliche Dinge zu übersehen, wie folgendes Beispiel zeigt:

Spring (1971) machte bei seiner vergleichenden Untersuchung der Anpassungen zweier Lummenarten *(Uria lomvia, U. aalge)* eine ausgezeichnete Analyse des Skelett-Muskel-Systems, stützte sich aber bei der ökologischen Interpretation weitgehend auf die umfangreiche Literatur über die beiden Arten. Folgende Anpassungen an den Nahrungserwerb der weiter nördlich verbreiteten Dickschnabellummen arbeitete Spring an Gefangenschaftsvögeln heraus: sie tauchen tiefer, aber weniger wendig als Trottellummen, sie sind bessere Langstreckenschwimmer und stabilere Schwimmer. Dies und ihr besseres Flugvermögen stehen in Beziehung zu ihrer Nahrungssuche in größerer Entfernung vom Brutplatz, in tieferem Wasser, im Rütteln, wodurch die Art vom Vorkommen pelagischer Fische unabhängig wurde. Die daraus resultierende Betonung des Brustabschnittes und der Vorderextremität bei der Dickschnabellumme sind unvereinbar mit gutem Gehvermögen, wie es die andere Art besitzt. Durch den Verzicht auf Freilandarbeit entging Spring die Feststellung einer möglichen anderen wichtigen bio-

Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell, Bundesrepublik Deutschland

logischen Rolle der längeren, größeren und weniger flächenbelastenden Flügel (Kartaschew 1960) der Dickschnabellumme, nämlich bei der Nutzung der artspezifischen Neststandorte (Flugmanöver beim Landen sind bei Rüppell 1971 dargestellt). Williams (1974) verglich Neststandorte und Verhalten der beiden Arten. Er fand, daß Dickschnabellummen stets direkt an ihren Nestern auf sehr schmalen Felssimsen „punktlanden" können, während Trottellummen, die in offeneren Situationen brüten, an unbesetzten Stellen landen und von dort zu ihren Nestern gehen. Während ihrer arktischen Entstehung dürfte die Dickschnabellumme starkem Selektionsdruck zur Nutzung schmaler Felssimse ausgesetzt gewesen sein. So wäre es notwendig zu untersuchen, welche Flügelmerkmale unter diesem Selektionsdruck entwickelt wurden und wie diese Anpassungen mit anderen (z. B. für Nahrungserwerb und Zug) zusammengewirkt haben. Das Beispiel zeigt, daß die Angepaßtheit einer Struktur nur zu verstehen ist, wenn alle ihre biologischen Rollen, die sie spielt, erkannt wurden, und daß eine biologische Rolle einer Struktur stets in Beziehung zu einem Selektionsfaktor der Umwelt gesehen werden muß.

Ich habe einen großen Teil des ökomorphologischen Schrifttums unter dem Gesichtspunkt durchgesehen, zu welchen Anteilen in den einzelnen Arbeiten deskriptive, funktionelle Morphologie bzw. Verhalten und Ökologie bearbeitet wurden. (Ein Verzeichnis dieser Literatur kann beim Autor angefordert werden.) Von wenigen Ausnahmen abgesehen, dominiert meist der morphologische Teil deutlich. Im folgenden möchte ich einiges zu den beiden Bereichen anmerken.

Ökologie und Verhalten

Wegen der unterschiedlichen Fragestellungen ist es nicht möglich, generelle Vorschläge zu machen, was bei Analysen der biologischen Rolle und ökologischer Faktoren untersucht werden soll. Bei Vögeln wurden hauptsächlich Anpassungen der Bewegungs- und Ernährungsweise analysiert.

Freiland

Hier fehlen noch, besonders bei vergleichenden Untersuchungen, Quantifizierungen ökologischer und ethologischer Beobachtungen (etwa Quantifizierungen bestimmter Nahrungserwerbtaktiken oder der Frequentierung bestimmter Orte der Nahrungssuche, Strata, Substrate). Durch den Einsatz neu entwickelter Meßmethoden (Vegetationsmessungen MacArthur & MacArthur 1961) und den Einsatz verschiedener Geräte (Stoppuhren, Tonband zur Registrierung, event-recorder, Cody 1968, Dawkins 1971) können viele ökologische und ethologische Beobachtungen auf eine quantitative Basis gestellt werden. In zunehmendem Maße können auch komplizierte technische Geräte wie spezielle Zeitlupenkameras unter Freilandbedingungen angewandt werden.

Laboratorium

Ein beträchtlicher Teil der Untersuchungen von Anpassungen sollte an Gefangenschaftsvögeln gemacht werden. An Vögeln, die unter naturnahen Bedingungen gehalten werden, lassen sich Beobachtungen machen und Registriermethoden anwenden, die im Freiland nicht durchzuführen sind. Ein großer Vorteil der Laboratoriumsarbeit ist, daß unter standardisierten Bedingungen beobachtet werden kann und daß im Experi-

ment bestimmte Bedingungen konstant gehalten, andere geändert werden können. An drei Schwirl-Arten *(Locustella)* habe ich zum Beispiel durch Filmanalysen, durch Experimente mit einen Hindernis und durch Herstellung von Fußspuren Unterschiede in der Bewegungsweise gefunden, deren biologische Bedeutung im Freiland geklärt werden konnte (Leisler 1977).

Eine schöne Kombination von Freiland- und Laboratoriumsuntersuchungen ist die Arbeit von Partridge (1976 a) über Nahrungserwerb und Nahrungstechnik einer nadelwald- bzw. laubwaldbewohnenden Meisenart (Tannenmeise, *Parus ater;* Blaumeise, *P. caeruleus*). Nach Freilandbeobachtungen nutzen die beiden Arten auf derselben Baumart unterschiedliche Substrate und suchen in unterschiedlicher Haltung nach Nahrung. Die Nahrungserwerbstechniken wurden im Freiland nur qualitativ erfaßt. Sie wurden an Gefangenschaftsvögeln in Experimenten mit künstlichen Bäumen und künstlichen Objekten, in denen versteckte Nahrung auf verschiedene Weise erreichbar war, untersucht. Artspezifische Geschicklichkeitsunterschiede beim Nahrungserwerb der beiden Arten konnten auf diese Weise festgestellt werden, ohne daß diese durch unterschiedliche Beutetiervorkommen oder unterschiedliche Beutetiertypen beeinflußt waren.

Morphologie

Obwohl der Konstruktionsanalyse die zentrale Stellung bei Untersuchungen von Anpassungen zukommt, wird bei vielen ökomorphologischen Arbeiten auf sie verzichtet. Statt dessen zieht man Ergebnisse an anderen Gruppen aus der Literatur heran. Die Auswirkungen auf die eigenen Untersuchungen bei solchem Vorgehen hängen davon ab, wie ähnlich die Strukturen sind und funktionieren bzw. wie ähnlich die biologischen Rollen sind, die sie erfüllen, und wie gut die Konstruktionsanalyse ist, auf die man sich bezieht. Gefahren bei derartigem Vorgehen drohen zum einen daher, daß von falschen oder unvollständigen Funktionsvorstellungen ausgegangen wird, zum anderen, vor allem bei Konstruktionen, die vielfältig eingesetzt werden (wie z. B. Hinterextremität, Schnabel), daher, daß nicht alles „Funktionieren" und alles „Fungieren" berücksichtigt wurde. Partridge (1976 b) untersuchte Beinlänge und -proportionen bei vier europäischen *Parus*-Arten: Sie war außerstande, ihre ökologisch-ethologischen Ergebnisse über die Bewegungsweisen mit den anatomischen Befunden in Einklang zu bringen. Ohne Konstruktionsanalyse übernahm sie die funktionelle Interpretation von allgemeinen Ergebnissen an anderen Gruppen, wie Baum- oder Bodenleben oder Hängen an Zweigen die Beinproportionen von Singvögeln beeinflussen. Für die Blaumeise, die am häufigsten in Rückenlage hängt, erwartete Partridge die kürzesten Tarsen, stellte aber nicht in Rechnung, daß nach ihren eigenen Befunden die Art häufig auch vertikale Substrate benutzt — eine Tatsache, die auch aus der Winterökologie der Blaumeise bekannt ist. So hätte eine Kompromißanpassung sowohl für Hängen als auch für Vertikalklettern erwartet werden müssen. Vernünftige Vorstellungen über Erfordernisse eines Klettervogels ohne Stützschwanz auf vertikalen Substraten besitzen wir erst seit dem Modell von Winkler & Bock (1976). Das Modell sagt voraus, daß in solchen Situationen der Besitz sehr langer, stark beugbarer Beine am günstigsten sein müßte. Berücksichtigt man diese Funktionserfordernisse, so wird die relativ große Tarsuslänge der Blaumeise verständlich. Derartige allgemeine Ergebnisse mußten häufig in ihrer Gültigkeit eingeschränkt und modifiziert werden: So haben bodenlebende

Singvögel gewöhnlich lange Läufe. Bei Fringilliden stellte jedoch FRETWELL (1969) fest, daß sich Arten, die häufig scharren, durch den Besitz kurzer Läufe auszeichnen.

Obwohl die Funktionsmorphologie in den letzten 30 Jahren große Fortschritte gemacht hat (BOCK 1974, 1977), fehlt es noch an funktionellen Analysen komplexer Skelett-Muskel-Systeme ähnlich den Untersuchungen der Hinterextremität (CRACRAFT 1971), des Flügels (BILO 1971, NACHTIGALL & KEMPF 1971) und des Schnabels (BOCK 1964, ZISWILER 1965, ZWEERS 1974).

Es fehlt weiter an Arbeiten, die neue Modelle beschreiben, an einfachen Arbeiten, bei denen eine Struktur geändert wird, um deren Wirkungsweise zu verstehen (z. B. RIEHM 1970), und an der Beschreibung natürlicher Experimente (Übersicht bei PARTRIDGE 1976 b).

Viele unserer Kenntnisse vom Funktionieren verschiedener Körperteile sind noch ungenügend oder falsch. Hier könnte der Einsatz multivariater Verfahren einigen Fortschritt bringen (WINKLER & LEISLER, in Vorbereitung). Das soll anhand einer Untersuchung der Flugapparatur einiger sich ökologisch wie systematisch nahestehender Sylviidengattungen (*Locustella, Acrocephalus, Sylvia,* 15 Arten) aufgezeigt werden. Das Großgefieder wurde anhand von Messungen von Flügel- und Schwanzfedern mittels einer Hauptkomponentenanalyse (PCA) analysiert. 18 nach dem derzeitigen Kenntnisstand funktionell bedeutsame Merkmale wurden berücksichtigt (s. Tabelle 1). Nach den Korrelationen mit den ursprünglichen Variablen lassen sich die Komponenten funktionsmorphologisch folgendermaßen interpretieren: Komponente I faßt Merkmale von Streckenfliegern zusammen, Komponente II Merkmale von extrem runden

Tabelle 1: Funktionskomplex „Flugapparatur"

Merkmal	Hauptkomponente (PC)			
	I	II	III	
1 Alula	0,42	—0,07	**0,66**	
2 Handschwinge X	—0,12	**0,88**	0,11	
3 Handschwinge IX	**0,75**	**—0,62**	0,16	
4 Handschwinge VIII	**0,98**	—0,15	0,02	
5 Handschwinge VII	**0,98**	0,19	—0,07	
6 Handschwinge VI	**0,90**	0,42	0,00	
7 Kerbe X	—0,37	**0,70**	0,14	
8 Kerbe IX	0,40	**0,63**	—0,48	
9 Kerbe VIII	0,34	**0,80**	—0,23	
10 Kerbe VII	0,22	**0,87**	—0,13	
11 Armschwinge 1	**0,75**	**0,61**	0,11	
12 Armschwinge 9	**0,69**	—0,34	0,50	
13 Schwanz	0,37	0,44	**0,74**	
14 Schwanzstufung	**—0,70**	—0,14	**0,63**	
15 Flügellänge — X	**0,74**	**—0,60**	—0,05	
16 Flügellänge — A1	0,38	**—0,78**	—0,09	
17 Schwanz/Flügel	—0,29	0,41	**0,76**	
18 Flügellänge	**0,97**	0,10	0,05	
Prozent der erklärten Varianz	40,7	30,8	14,5	Gesamt 86,0

Flügeln mit hoher Manövrierfähigkeit. Die Merkmale von Komponente III lassen sich so interpretieren: Ausgeprägte Alulae funktionieren als Hochauftriebserzeuger bei hochangestellten Flügeln beim Langsamflug und beim Landen (Nachtigall & Kempf 1971), der Schwanz erfüllt verschiedene Aufgaben.

Die Ansichten über das Funktionieren der aufgefächerten Handschwingen und ihr Zusammenwirken mit der Alula sind kontrovers (Kokshaysky 1977). Savile (1957) und Brown (1963) nehmen an, daß beide zusammenwirken und „the two together do make a functional propelling wing tip, which can operate at high angles of attack and thereby develop large lift at low speeds“ (Brown 1963). So hätte man Alula und Kerben der Handschwingen in einer Komponente erwarten müssen, während sie tatsächlich in zwei verschiedenen liegen. Dies könnte bedeuten, daß hier falsche Funktionsvorstellungen vorliegen.

Tatsächlich hat Hummel (1980) gezeigt, daß aufgespaltene Flügelspitzen die Längsstabilität erhöhen, bei begrenzter Spannweite den induzierten Widerstand reduzieren, den Schub möglichst groß machen, aber den Maximalauftrieb nicht erhöhen. Sie wirken also nicht wie der Daumenfittich, was völlig mit den vorliegenden Befunden übereinstimmt.

Durch derartige Analysen können also konkrete Fragen an Funktionsmorphologen formuliert werden, das Funktionieren einer oder das Zusammenwirken mehrerer Strukturen bei der untersuchten Gruppe zu klären.

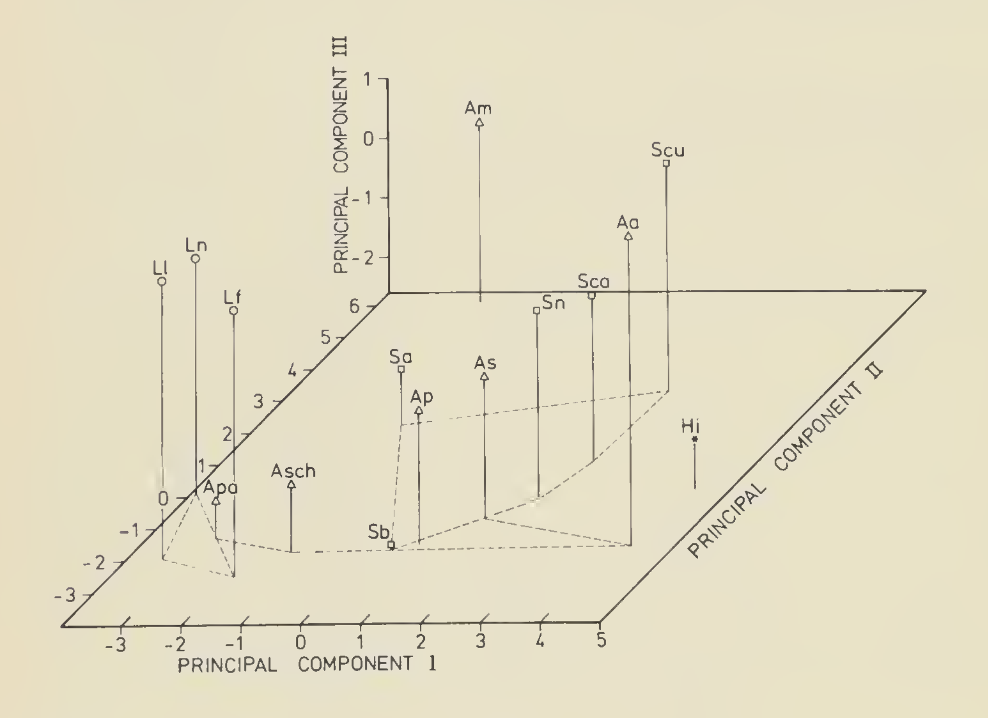


Abb. 1. Hauptkomponentenanalyse von 18 Merkmalen des Funktionskomplexes „Flugapparatur“ einiger mitteleuropäischer Sylviinen. Korrelationen der 18 Merkmale mit den ersten 3 Hauptkomponenten in Tab. 1. Komponente I repräsentiert zunehmende Eigenschaften von Streckenfliegern, Komponente II zunehmende Eigenschaften von Eckenfliegern, Komponente III bedeutet zunehmende Schwanzlänge- und -stufung und zunehmende Alulalänge.

Abkürzungen und Symbole: *Locustella* = o, Ll = *L. luscinioides,* Ln = *L. naevia,* Lf = *L. fluviatilis, Sylvia* = □, Sa = *S. atricapilla,* Sb = *S. borin,* Sn = *S. nisoria,* Sco = *S. communis,* Scu = *S. curruca, Acrocephalus* = △, Ap = *A. palustris,* Apa = *A. paludicola,* Asch = *A. schoenobaenus,* Aa = *A. arundinaceus,* As = *A. scirpaceus,* Am = *A. melanopogon,* * = *Hippolais icterina.*

Ordination of some Central European Sylviid warblers on the first three principal components constructed by analysis of 18 characters of the flight apparatus. Correlations between original characters and principal components are shown in Tab. 1. Component I represents increasing qualities of high performance fliers, component II increasing qualities of thicket fliers, component III represents increasing length of tail and alula and graduation of tail.

Weiter können sich durch den vergleichenden multivariaten Ansatz Hinweise auf verschiedene biologische Rollen einer Struktur bei einzelnen Arten ergeben. Beispiel: In Abbildung 1 ist die Ordinierung der untersuchten Einheiten nach den Merkmalen zunehmende Spitz- und Langflügeligkeit (PC I), zunehmende Rundflügeligkeit (PC II), zunehmende Schwanz-, Alulalänge (PC III) dargestellt. Schlechte Flieger würden sich links unten finden, das sind die *Locustella*-Arten und der Seggenrohrsänger *(Acrocephalus paludicola)*. Bei der Beziehung von Komponente I und III läßt sich erkennen, daß bei der Mehrzahl der Arten mit zunehmender Lang-, Spitzflügeligkeit die Schwanz-, Alulalänge zunimmt. Einzelne Gruppen oder Arten weichen von diesem Trend ab, folgen also anderen adaptiven Wegen, z. B. die Schwirle *(Locustella)*. Diese Gruppe hat bei schlechter Flugfähigkeit sehr lange gerundete Schwänze. Das legt nahe, daß der Schwanz bei ihr andere Funktionen erfüllt als bei den anderen untersuchten Gattungen. Wahrscheinlich wirkt er bei den Schwirlen eher als Balancierorgan und spielt eine wichtige biologische Rolle beim Durchschlüpfen der dichten Vegetation (Gaston 1974). Derartige Hinweise können dann in gezielten Studien überprüft werden.

Danksagung

Herrn Dr. Winkler (Wien) danke ich für die Berechnung der multivariaten Statistik.

Summary

Comparative field and laboratory analysis of ecological morphology

An adaptation can only be analysed sufficiently if the faculty as well as the biological role of a trait are known. As an inference from a biological role of a structure to its function is not possible, it is obvious that only a combination of laboratory and field work can be successful.

The central theme of ecomorphology is how single features or functional units in single taxonomic groups (species, genus) or ecological groups (guilds, communities) or in groups of convergent organisms (ecological equivalents) contribute to the fitness of the respective organisms. Difficulties in assessing the biological role of a feature arise from the fact that almost all parts of an organism are a result of compromises and that they are strongly interdependent. Therefore a broad knowledge of the entire life history of the species investigated is necessary. Thus adaptations are analysed best in integrated studies. A review of ecomorphological papers shows that the many gaps still left in our knowledge stem from the lack of appropriate ecological and quantitative behavioural data and from the failure to combine field and laboratory work.

Often species specific behaviour is to be ascertained more easily in captive birds under standardized experimental conditions than in the field. In a comparative approach similarities or contrasts between closely related species often help to clarify biological roles in individual species. It is risky to leave out a proper functional analysis of a structure and to infere its functional interpretation from general results on other groups. Our knowledge of the functioning of some structures is often insufficient or incorrect. Here the application of multivariate methods might bring some progress. Principal component analysis of several characters of one functional unit can yield a more detailed picture of functional interrelations. Moreover it can reveal still unknown correlations of characters.

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Uses of Adaptational Analysis in Evolutionary and Phylogenetic Study

V. ZISWILER

All our lectures so far have shown that morphology represents a fundamental branch of ornithology, which—contrary to widespread opinion—still faces a multitude of unsolved problems. Functional morphological research can be an end in itself, but it can also render decisive information in other fields such as systematics and phylogeny. Most of all, however, it can serve in a most important way to bring to light and help us understand patterns of evolution both in general and in detail (ZISWILER, 1977).

I would like to show how this can be done by illustrating directly out of our own field of research. Having convinced ourselves that the most important evolutionary trends amongst birds lie in the region of food-specialization, we have been trying to reconstruct evolutionary processes by making comparative and functional-anatomical investigations in the entire alimentary tract. We already have results of more than 10 higher taxa at hand, and our methods have now become almost standardized (GÜNTERT & ZISWILER, 1972; HOMBERGER & ZISWILER, 1972; HOMBERGER, 1979; ZISWILER, 1964, 1965, 1967 a, b, c, 1968; ZISWILER & FARNER, 1972).

One important area of research is devoted to questions concerning the favourite food of a certain species, how exclusively this species is bound to a favourite food, and how far this species has moved away from a more omnivorous state. We try to answer these questions in various ways, namely by field observation, by investigating the crop and stomach contents, and also by studying the food-preference of birds in captivity. By directly observing and examining the stomach contents of parrot-finches *(Erythrura)* we were able, for example, to prove that within these species certain types are extremely specialized in their feeding habits. *E. kleinschmidti* and *E. cyaneovirens regia*, for example, live almost entirely on the fruit and seeds of various *Ficus* species—this comprises 90 % of their diet—whereas *E. hyperythra* feed specifically on bamboo seeds (ZISWILER, GÜTTINGER & BREGULLA, 1972). Food-preference tests on more than 150 species showed us that the fringillids (Fringillidae) choose to eat mainly herbal seeds (dicotyledons), whereas emberizids (Emberizidae), ploceids (Ploceidae) and estrildids (Estrildidae) prefer to eat gramineous seeds.

Once we have discovered in what way a certain species has become specialized, we then try to determine what functional capacities a bird must develop in order to recognize favourite food, acquire it and digest it in the most rational way possible. Thus it became evident in the case of granivorous birds that they should find some way of opening the kernels before swallowing them. With the aid of slowmotion films we were able to discover that songbirds have developed two completely different methods for opening the seeds; the fringillids slice them open and the emberizids, ploceids and estrildids squeeze them out of the shell. Correlated with these highly specialized functions we further postulated that there are subtle tactile control-devices in the tongue and bucal regions (KRULIS, 1978; ZISWILER & TRNKA, 1972).

Another important functional area is food storage. Seeds are never found evenly dis-

Zoologisches Museum der Universität, Künstlergasse 16, CH-8006 Zürich, Schweiz

tributed over a biotope; they are irregularly distributed wherever there are seminiferous plants. Hence a granivorous bird which has discovered a source of food must find a way of gathering as many seeds as possible at one time. Here the problem arises of how to store the food in the area between the pharynx and the glandular stomach. Furthermore, if, when bringing up its young, such a bird does not want to adjust itself to eating insects, which are more evenly distributed and which can be carried by the parent bird in its beak to the nest, there ist the additional problem of how to regurgitate the stored seeds.

Other functional areas which demand special adaptations from granivorous birds are, for example, the preparation of a specific spectrum of digestive enzymes, the increased mucus production in the esophagus to facilitate the passage of the somewhat dry seeds, and the increased resorption ability of the mucosa of the intestine.

Once we have recognized a specific functional area connected with food-specialization, we then turn to the morphological structures, which had to be adapted in order to make a particular function possible. In the case of the above-mentioned special functions among granivorous birds, the following structures proved to be especially interesting: The horny palate and mandible of those songbirds which slice open and those which squeeze out seeds show different specific structures. The "slicers" have in their palate deep furrows, which converge at the front in order to wedge in the seeds; also the mandible has razor-sharp edges. The "squeezers" on the other hand press the seeds out with one or both of their blunt mandible edges against specially constructed abutments, protruding bulges or saddle-like elevations. This method also requires the tongue to support the seed, and this calls for special stiffening devices. This stiffness, incidentally, was acquired by different families in different ways. The ploceids (Bock & Morony, 1978) and estrildids developed special sesamoid bones independent of the Ossa entoglossa; estrildids and some fringillids, on the other hand, stiffen their tongue even more by swelling the venous sinuses in a similar way to the erection of the penis of a mammal.

This complicated method of opening seeds demands constant tactile control. Our search for the relevant sensory receptors led us to discover not only new types of sensory corpuscles but also the specific functional patterns of distribution of these corpuscles.

In the case of crows, different types of pharyngial pouches or a stretchable esophagus take over the above-mentioned storage function (Bock, 1961, 1973); in the case of the fringillids, emberizids, ploceids and estrildids, it is always an expandible portion in the mid-esophagal area, the crop. The histological examination of these crops led us to discover that even here among these four groups there are fundamental differences. The emberizids and ploceids have crops for storage only—the food cannot be regurgitated; the former have spindle-shaped crops, the latter can develop huge sack-like diverticula. The muscle-layers of the crop wall are identical to those of the rest of the esophagus.

The crops of the fringillids have an entirely different structure. The circular muscle layer of the muscularis propria is three times thicker than the rest of the esophagus wall, and 50 % of it contains striated multi-nuclear fibres. This very special formation is closely connected with the feeding habits of the fringillids, which feed their young by

regurgitating the crop contents in small portions by means of a short jerky movement. This regurgitation is possibly caused by a single contraction of the powerful circular muscle layer, whereas the subsequent dilatation of the crop is possibly a passive movement.

In the case of the estrildids, it is not only the circular muscle layer which is very thick but also the interlongitudinal muscle of the muscularis mucosae; these two muscle systems built crosswise against each other suggest an antagonistic function, which is confirmed by the singular way in which the estrildids feed their young. The adult bird clasps the beak of the young bird in its own and the food is transferred by a prolonged pumping action. We surmise that in this process the circular muscle is responsible for the contraction and the interlongitudinal muscle for the dilatation of the crop.

For me personally, the most fruitful research area connected with the tracing of evolutionary paths is the search for principles which determine the increase of the epithelial surfaces. The granivorous birds adapted themselves morphologically in this respect by increasing the efficiency of the mucus-producing esophageal glands on the one hand, and by enlarging the resorptive inner surface of the intestines on the other. In the case of the esophageal glands, our granivorous birds developed very different methods. The emberizids, which possess simple tubular glands like insectivorous or fructivorous birds, increased the number of glands by three times the normal amount. The fringillids increased the working capacity of their gland system by linking up various single glands to multi-lobar complexes with a common duct system, whereby the duct system is equipped with a special stratified epithelium. Finally the more omnivorous forms of ploceids and estrildids possess alveolar glands, which are subdivided in the exclusively granivorous birds by septa of connective tissue subdivding them into separate chambers.

As opposed to the insectivorous and fructivorous birds, all granivorous birds show a general tendency to increase their resorptive intestinal surface as much as possible. There are many different ways of doing this: nevertheless we have still been able to trace the way back to the basic pattern, which consists of a zigzag fold surface. Within the crow family we have a particularly fine example of such a line of development from interrupted zigzag lamellae via displaced lamellae right up to a hexagonal honeycomb pattern.

What can we conclude from all these morphological findings?

Our most significant conclusions are the negative ones, that is to say, when we can prove that two forms or groups have reached a form of specialization by means of entirely different functional and morphological adaptations, then this specialization indicates convergence. To return to our granivorous birds: If, for example, the fringillids slice the seeds open, whereas the estrildids squeeze them out, if the ploceids stiffen their tongue by developing a sesamoid bone, whereas the estrildid pump their tongues with venous blood, if the emberizids increase the number of their esophagus glands threefold, whereas the ploceids subdivide them into separate chambers, we can conclude that each of these four groups evolved from different omnivorous or insectivorous ancestors, especially if we consider that these groups differ not only in the characteristics we have mentioned, but that they differ from each other in 117 out of 150 characteristics which have been compared.

And now the positive conclusion. If two different forms or taxa have developed the same secondary adaptations in order to meet the requirements of a certain kind of specialization, this indicates that they could somehow be closely related. I must add that a positive assumption such as this is not as conclusive to the same extent as the negative one, since there is always the possibility that these adaptations are merely convergences. However, the more similarities we can ascertain when comparing different forms, the more likely it is that we can come to a positive conclusion. This method enables us to classify taxonomically disputed forms. It has helped us, for example, to relate the brambling and the chaffinch to the family of the fringillids, the snow-finch and the viduinae to the family of the ploceids.

By making detailed, complex functional-morphological analyses of certain specific adaptations over a wide spectrum of forms we have even been able to reconstruct complete evolutionary tracks. This is possible when we can show that a series of forms developed a considerable number of similar functional or morphological adaptations in their attempt to specialize in a certain way. We have, for example, been able to trace such evolutionary tracks amongst the genus of parrot-finches. Forms such as *Erythrura psittacea, E. pealii, E. cyaneovirens* and *E. regia* show an increasing tendency to limit their nourishment from granimeous seeds specifically to herbal seeds, and again from herbal seeds specifically to a diet comprising almost entirely of fig seeds. This specialization is accompanied by the adaptational readjustment from squeezing seeds out of the shells to slicing them open, and also by an increasing complication of the structure of the compound glands of the glandular stomach and the inner surface of the intestines. At the same time the discovery of this evolutionary process has helped us to reconstruct the distribution of the parrot-finches in the South West Pacific area, which led from New Guinea via New Caledonia—Fiji—and Samoa back to the New Hebrides.

To summarize, I would say that functional morphology is still the most fruitful and reliable source of information for an omnispective and phylogenetically orientated taxonomy.

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SYMPOSIUM ON
NEUROENDOCRINOLOGY AND ENDOCRINOLOGY
GENERAL ASPECTS AND THE CONTROL OF REPRODUCTION

7. VI. 1978

CONVENERS: A. OKSCHE, I. ASSENMACHER AND B. K. FOLLETT

The Neuroanatomical Basis of Avian Neuroendocrine Systems

A. Oksche

Nerve cells with both neuronal and secretory properties form the basic elements of neuroendocrine systems (Bargmann, 1977; Scharrer, 1978; Scharrer & Scharrer, 1963). Due to their neuronal nature they must be considered as integral components of the neuronal machinery of the brain. The secretory activity of these cells is characterized by the elaboration of granular material within the Golgi complex. Biologically active peptides or biogenic amines may be bound to such materials. Only neurosecretory messengers that enter the vascular compartment and act on remote target organs qualify as neurohormones. Other neuroendocrine cells contact their target cells directly and exert a neurohumoral influence via their neurotransmitters or neuromodulators. Thus, the neuroendocrine apparatus transforms nervous signals into chemical messages and forms a link between the nervous and endocrine systems. Although an essential part of the neuroendocrine system is concentrated in the hypothalamus, it is not the only site of neuroendocrine activity in the vertebrate brain.

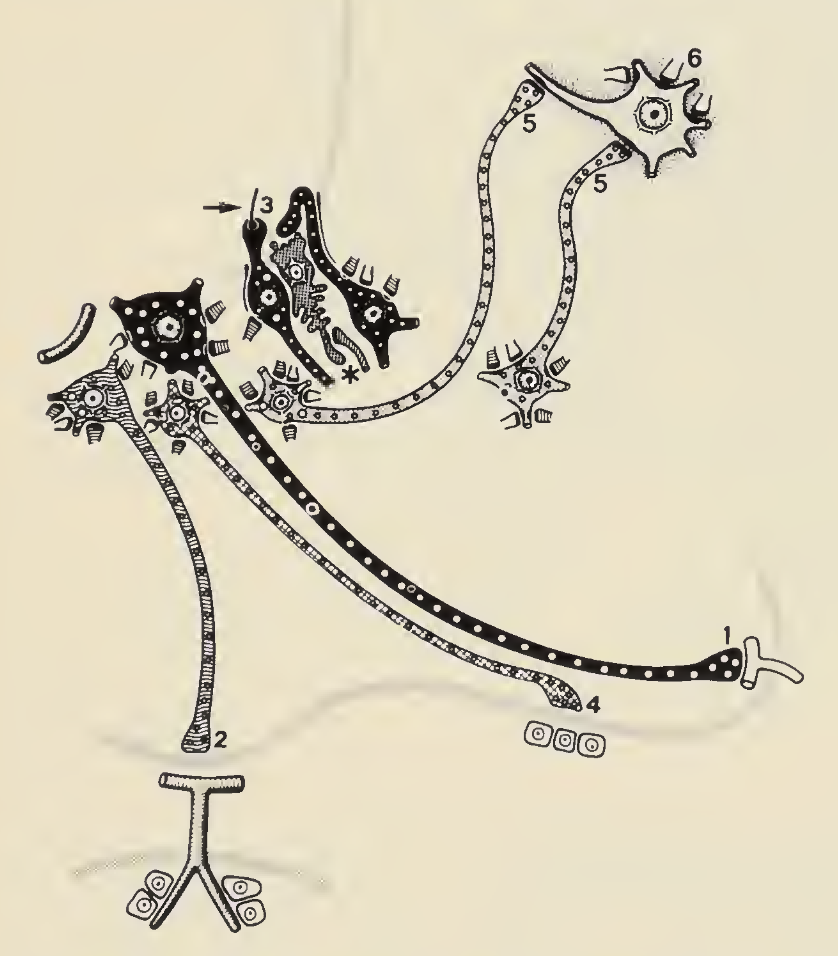


Figure 1. Basic neurosecretory mechanisms in the avian brain. 1: Release of neurohormones into the general circulation (posterior lobe system). 2: release of neurohormones into the portal circulation of the hypophysis (anterior lobe system). 3: release of biologically active agents into the cerebrospinal fluid (circumventricular organs): → = outer segment of a sensory neuron, * = ependymal tanycyte. 4: neurohumoral contact with epithelial cells (pars tuberalis). 5: synaptic contact (release of neurotransmitters or modulators). 6: conventional neuron. Afferent fibers form multiple axo-dendritic and axo-somatic synapses with neurosecretory neurons. (Drawing by D. Vaihinger).

Since birds have evolved from archosaurian reptiles and mammals from mammal-like reptiles, the reptilian brain provides the key for comparing avian and mammalian central nervous systems (Oksche, 1976). The avian hypothalamo-hypophysial axis has attained a high degree of morphological and functional specialization, by no means

Zentrum für Anatomie und Cytobiologie der Justus-Liebig-Universität Aulweg 123, D—6300 Gießen, Bundesrepublik Deutschland

inferior to that observed in mammals (OKSCHE & FARNER, 1974; OKSCHE, 1977). However, in contrast to the mammals, the birds still possess conspicuous groups of cerebrospinal fluid-contacting neurons which are concentrated in the nonciliated areas of circumventricular organs (STERBA & BARGMANN, 1977) (Fig. 1). Some of these organs have the characteristics of sensors, others are dominated by secretory elements. The majority of the avian circumventricular organs are located within the hypothalamus. The latter extends from the lamina terminalis to the mammillary body.

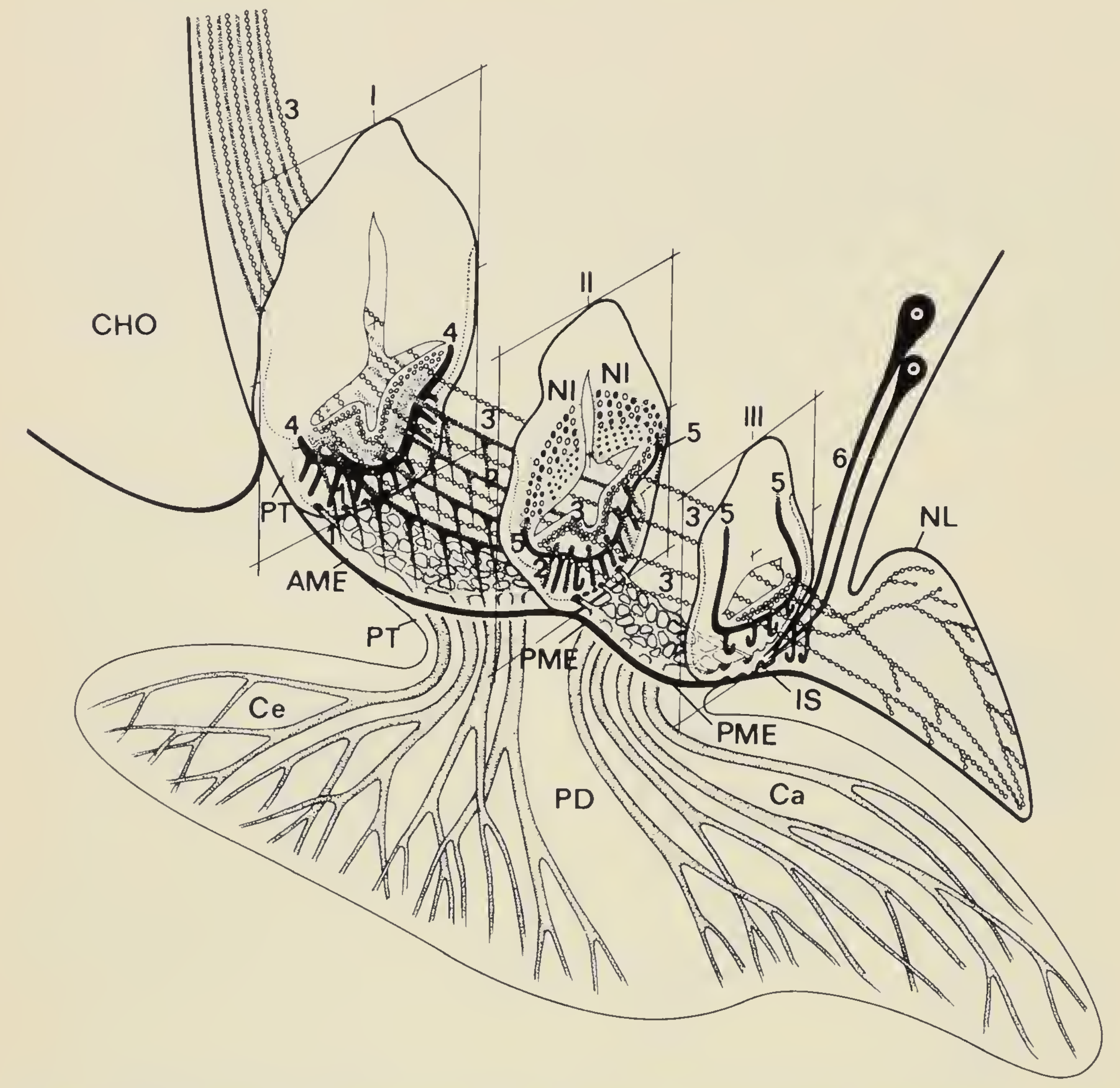


FIGURE 2. Diagrammatic representation of the hypothalamo-hypophysial connections in a passerine bird *(Zonotrichia leucophrys gambelii)*. Note particularly the neurohemal sites: NL neural lobe, AME anterior median eminence, PME posterior median eminence, and the Neurosecretory pathways: 1, 2 pathways from the rostral hypothalamus to the AME; 3 pathway to the neural lobe; 4, 5 sequential pathways from the mediobasal hypothalamus to the AME or PME. Note the portal vessels to the pars distalis (PD). CHO optic chiasma. (For further details, see OKSCHE & FARNER, 1974; courtesy Springer-Verlag).

For structural and functional reasons the hypothalamus can be subdivided into rostral (preoptic and supraoptic) and caudal (tuberal) portions. There are two major sites for release of hypothalamic neurohormones: (i) the neural lobe of the hypophysis, and (ii) the median eminence with its anterior and posterior divisions (Fig. 2). Patterned

bundles of axons bearing specific agents are directed toward these neurohemal organs. However, not all of the secretory neurons of the rostral and tuberal hypothalamus are connected with neurohemal areas. Their axons may also project to extrahypothalamic sites to terminate synaptically on ordinary neurons (neurotransmitter or modulator type of action) (Fig. 1). Since immunocytochemistry and microfluorimetry have opened up new prospects for the selective identification and mapping of secretory neurons, the classical typology of magnocellular and parvocellular elements has become less important.

Immunocytochemical studies have shown that, by analogy with vasopressin- and oxytocin-producing cells of mammals, vasotocin and mesotocin are produced in separate neurons of the avian hypothalamus (Starling, Zebra Finch, Japanese Quail). The distribution of vasotocin and mesotocin neurons follows a discrete pattern characterized by a different ratio of both neuronal types in the single subdivisions of the classical magnocellular nuclei (Goossens et al., 1977). Vasotocin neurons are dominant in the rostral portion of the supraoptic nucleus. Mesotocin neurons are most conspicuous in the lateral part of the supraoptic nucleus and especially in the paraventricular nucleus. The pathway to the neural lobe contains vasotocinergic and mesotocinergic fibers, and the neural lobe, consequently, a speciesdependent pattern of both types of terminals. In contrast, the external zone (palisade layer) of the anterior median eminence, which stains selectively with all dyes of the Gomori type, contains only vasotocinergic fiber elements (Calas, 1974; Goossens et al., 1977; Bons et al., 1978). However, at the electron microscopical level, the elementary granules of the external zone are considerably smaller in diameter than those of the neural lobe: 130—180 nm (average 150 nm) versus 200—250 nm. By analogy with mammals and on the basis of some experimental evidence in birds, it may be that the immunoreactive material of the external zone is closely correlated to or even identical with the corticotropin releasing factor (CRF). The latter is released into the portal circulation and transported to the anterior lobe (pars distalis) of the hypophysis. It may be produced in specialized periventricular neurons of the supraoptic and paraventricular nuclei.

In contrast to the vasotocinergic elements of the palisade layer, which are restricted to the anterior median eminence, LHRH-immunoreactive fibers occur in both subdivisions of the avian median eminence (domestic Mallard, Japanese Quail). In addition, the lamina terminalis is a target site of these fibers. To date, the corresponding LHRH-immunoreactive perikarya have been found exclusively in the preoptic hypothalamus (Bons et al., 1977, 1978; Oksche, 1978). As there is strong experimental evidence that the basal tuberal hypothalamus plays a major role in gonadotropic regulation, or even in production of gonadotropinreleasing hormone(s), the problem of the hierarchy and interplay of gonadotropic centers still remains enigmatic (Yokoyama et al., 1978).

Immunocytochemical proof for a TRH-system in birds is lacking.

The avian hypothalamus (domestic mallard) is rich in somatostatinimmunoreactive neurons. The perikarya of these cells are located in the vicinity of the lamina terminalis and along the supraoptic and paraventricular nuclei (Blähser et al., 1978). In the anterior portion of the paraventricular nucleus they may be intermingled with vasotocin- and mesotocin-immunoreactive cells. The axons of somatostatin neurons project to an

extensive area of the external zone of the median eminence, especially to its rostral division.

In contrast to mammals, the basal tuberal hypothalamus of birds is free of microfluorimetrically-detectable dopamine neurons (Oksche & Farner, 1974). Aminergic perikarya occur, however, in the paraventricular organ (dopamine and serotonin neurons) and around the preoptic recess.

The anterior median eminence receives a conspicuous axonal input from the rostral, pretuberal and tuberal hypothalamus, whereas the posterior median eminence is supported by multiple, serially arranged tuberal systems (Oksche & Farner, 1974; Fig. 2). These systems, at least in passerine birds, may establish point-to-point connections with the hypophysial portal circulation. Only a part of these fiber systems has been identified by immunocytochemical and microfluorimetric methods. In birds, the tuberal and rostral portions of the hypothalamus are extremely rich in neuronal perikarya containing different types of electron microscopically-detectable elementary granules. Apparently, the avian hypothalamus produces different, to date only partly identified, peptides with a wide range of biological properties. After the discovery of endorphins, enkephalins and other brain peptides, the concept of the peptidergic neuron has been considerably extended (Scharrer, 1978). In contrast to mammals, these new aspects have not been elucidated in birds.

Additional information is also needed with respect to the ascending noradrenergic systems that have been thoroughly investigated in mammals. In birds, noradrenergic fibers originating in the lower brainstem supply the centers of the tuberal and the rostral hypothalamus. The phylogenetically archaic periventricular region of the avian hypothalamus is extremely rich in noradrenergic afferents (Hartwig, 1975).

The noradrenergic elements in the median eminence apparently belong to the ascending brainstem system (Calas, 1974; Hartwig, 1975). However, we have yet to understand the neuronal and tanycytic (glial) apparatus of this neurohemal region. Principally, peptidergic and aminergic elements may interact at the level of the neuronal perikarya in the nuclear area, and/or at the level of the axon terminals in the external layer of the median eminence. To date, this problem has not been resolved. In addition, experimental evidence in birds does not speak in favor of a significant role for the tanycytes in the transport of gonadotropic neurohormones across the median eminence, at least under physiological conditions (Uemura & Kobayashi, 1977). On the other hand, the aminergic innervation of tanycytes does have an effect on the uptake of tracer molecules from the cerebrospinal fluid (Nozaki et al., 1975).

This general neuroanatomical review may serve as a topographical and structural basis for the analysis of the role of the rostral and tuberal hypothalamus in the photoperiodic control of gonadotropin secretion. Further, it may promote discussion of the “encephalic photoreceptor(s)”, circadian oscillators and the mechanisms of “biological clocks” (Yokoyama et al., 1978). In photoperiodic responses of birds, time and photosensitivity must be considered, the latter depending on circadian components within the mechanism (Farner et al., 1977).

Since this symposium is focussed on problems of the hypothalamohypophysial axis, the pineal body, a self-sustaining circadian oscillator and, at the same time, an important circumventricular neuroendocrine organ, has been excluded from the present com-

munication (see GWINNER, 1980; HARTWIG, 1980; MENAKER, 1980). The most complex circumventricular organs, e. g. the subfornical organ, may encompass sensors and neuroendocrine effectors (STERBA & BARGMANN, 1977). The receptor apparatus of these organs may be controlled by peptidergic and aminergic afferents and act on hypothalamic centers involved in regulatory mechanisms. Unfortunately, the problem of the central nervous projections of circumventricular organs has been overlooked by many neurobiologists.

With the new functional implications in mind, the classical scheme of the hypothalamic nuclei as anatomical and functional units appears to be too rigid. Therefore, in an attempt to elucidate the intrinsic organization of the avian hypothalamus, a new concept should be presented (OKSCHE & FARNER, 1974; OKSCHE, 1976, 1977). In the avian hypothalamus cluster-like groups of neuronal perikarya and the afferents of these cell complexes are arranged in a patterned manner. Among the reptiles, the cluster-like subunits first become conspicuous in crocodiles and snakes.

The subunits of the hypothalamic nuclei are formed by steroid-binding neurons, nerve cells producing different types of neurohormones and neurotransmitters, interneurons, intrinsic collaterals and afferents of differing origin, including limbic and ascending aminergic projections. These structural elements are embedded in highly specialized zones of the neuropile, rich in patterned arrangements of synapses. This synaptic apparatus may be essential for a guided propagation of excitation along certain channels and circuits. Further, it may provide the anatomical basis for convergence and divergence, integration of external and internal information and finally for functional isolation of, or interaction between, spatially adjacent neuronal systems. Thus, gonadotropic, thermoregulatory, osmoregulatory and dipsogenic systems might function properly in spite of their location within a minute hypothalamic area. Their netlike spatial arrangements, displaying local nodular aggregations of functionally related neurons, appear to be consistent with the concepts of neuronal networks. The increasing functional complexity of the hypothalamus depends primarily on the proliferation of neuronal clusters, the differentiation of specific synaptic patterns and the formation of highly organized integrative centers.

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Monoaminergic and Peptidergic Systems of the Avian Hypothalamus (with Special Reference to the Median Eminence and the Organum Vasculosum Laminae Terminalis)

A. Calas and O. Bosler

Introduction

Photoperiodic avian species such as the duck are good models for the study of neuroendocrine mechanisms (Benoit & Assenmacher, 1955; cf. Follett, 1973). A key area in these mechanisms is the hypothalamic median eminence (ME). In birds, the primary plexus of the hypophyseal portal system lies only on the surface of the median eminence, allowing a clearcut distinction between an inner zone where bundles of aldehyde-fuchsin (AF) positive peptidergic fibers directed to the neural lobe are localized, and an outer region containing endings of neurosecretory adenohypophysiotropic axons (AF + in rostral part, AF — in the caudal part). This simplified anatomical organization has generated many cytophysiological studies of this neurohemal area with special reference to its monoaminergic (MA) and peptidergic innervation (Sharp & Follett, 1970; Warren-Soest et al., 1973; Calas, 1975; Goossens et al., 1977). More recently, morphological and cytophysiological studies have been carried out on another circumventricular structure, the organum vasculosum laminae terminalis (OVLT) which lies with respect to the optic chiasma in the same relative position as the ME (Mikami 1976; Bosler, 1977). In the present paper, we summarize data collected in our laboratory on the duck ME and OVLT and discuss their monoaminergic and peptidergic innervations.

Material and methods

Most of the investigations have been carried out in adult male Peking ducks, *Anas platyrhynchos*. Some data have been also collected from adult male quails, *Coturnix coturnix japonica* and pigeons, *Columba livia domestica*. Monoaminergic innervation was first studied by standard fluorescence histochemistry after pharmacological inhibition of monoamineoxidase and, in some cases, after tryptophan pretreatment. Some of the preparations were then analyzed by microspectrofluorimetry (Calas et al., 1974). Owing to the limitations in resolution of the histofluorescence technique and its poor sensitivity for the detection of serotonin, we have also examined the monoaminergic innervation of the two organs using a radioautographic technique (Aghajanian et al., 1966; Descarries & Droz, 1970): tritiated noradrenaline (^{3}H-NA) and serotonin (^{3}H-5 HT), when administered in vitro or by an intracerebroventricular (ICV) route, are taken up and retained by specific monoaminergic fibers selectively thus allowing their histological and ultrastructural radioautographic identification (Calas, 1973; Calas & Ségu, 1976). Peptidergic innervation has been investigated by immunocytochemical techniques using antisera (AS) against LH-RH or vasotocin (AVT) (Calas et

Département de Neurobiologie cellulaire, Institut de Neurophysiologie et Psychophysiologie, C. N. R. S., 13274 Marseille cedex 2, France.

al., 1973, 1978). The reactive sites were detected on histological sections by use of the indirect immunofluorescence or PAP methods. For electron microscopy, two different procedures were used: formaldehyde-fixed thick sections were exposed to the specific and then the peroxidase-conjugated AS before embedding (Tougard et al., 1973) or thin sections of glutaraldehyde-fixed and embedded material were treated with diluted specific AS and then with the PAP procedure (Sternberger et al., 1970).

Results and discussion

Morphological features

The duck's ME and OVLT constitute thin structures which close the third ventricle at the level of the infundibular and preoptic recesses respectively. Both display the characteristical features of neurohemal organs: 1) a vascular supply composed of a well-developed network of superficial fenestrated capillaries together with a few unfenestrated internal capillaries; 2) neurosecretory axons sometimes reaching the external parenchymal basement membrane. These can be divided into several groups according to the different kinds of dense granules and/or vesicles which they contain; 3) non-ciliated stretched ependymocytes linking the ventricle to the external vessels (tanycytes). In addition, the two organs contain numerous glial cells generally located in the inner ME and OVLT and emitting processes which can reach the external basement membrane. Neuronal perikarya displaying scattered neurosecretory granules are also encountered in the subependymal layers.

The presence of neurosecretory fibers together with fenestrated capillaries is characteristic of neurohemal areas where a neuroendocrine function can also be carried out by tanycytes. In the present paper, we shall refer exclusively to the identification of nerve fibers. Tanycyte function in the duck's ME and OVLT has been discussed elsewhere (Calas, 1975; Bosler, 1977).

Monoaminergic innervation

In the ME, fluorescence histochemistry revealed a dense internal plexus of green fluorescent fibers containing NA (as demonstrated by subsequent microspectrofluorimetric analysis, Calas et al., 1974). These fibers sometimes surrounded non-reactive cell bodies. In the external ME a more diffuse and weak reaction was observed: scarce dopamine (DA)-containing fibers were identified by microspectrofluorimetry in the external ME but no DA-containing neuronal perikarya could be detected within the hypothalamus. After loading with tryptophan, distinct yellow fluorescent fibers which displayed the spectral characteristics of 5 HT could be seen (Coll. H. G. Hartwig). The monoaminergic innervation of the OVLT was less developed. It was composed of green fluorescent fibers, probably containing NA. Although widely distributed in the caudal part of the lamina terminalis, these were less numerous and preferentially located within the inner layer in the rostral part. These results have been confirmed and extended to the electron microscope level using the radioautographic approach. Following an ICV injection of ^{3}H-NA, axonal varicosities containing numerous clear vesicles (sometimes displaying an eccentric core) and some large granular vesicles (LGV) were labeled in the inner ME and in the inner OVLT. They are probably noradrenergic in view of their internal localization and the general failure of the radioautographic

technique to demonstrate DA fibers (Calas & Ségu, 1976). These NA fibers sometimes formed symmetrical or asymmetrical synaptic contacts with dendrites (ME, OVLT) or cell bodies of neurosecretory neurons (ME). They could be selectively destroyed by ICV 6-OH-DA (Calas, 1973).

^{3}H- 5 HT was administered under conditions which allow its specific uptake by 5 HT terminals (Descarries et al., 1975). Axons labeled in these conditions were localized essentially in the outer ME and in the lateral regions of the lamina terminalis. They were smaller in diameter than the noradrenergic ones and their varicosities displayed more LGV. They could be destroyed by ICV 5, 6-DHT (Calas, 1975). In the ME, they occasionally reached the basement membrane or tanycyte processes, and showed in the latter case synaptoid differentiations. True synapses were only found in the OVLT between a few labeled axons and dendrites or dendritic spines. The results of histofluorescence, microspectrofluorimetry and radioautography demonstrate a different pattern for NA and 5 HT fibers in the two organs where they seem to play distinct roles. The synaptic NA innervation of infundibular neurons and synaptic NA and 5 HT terminals in the anterior hypothalamus might constitute the morphological basis for a function in various neuroendocrine mechanisms (Follett, 1973; McNeill et al., 1975). Furthermore, 5 HT might also exert in the ME a non-synaptic control of tanycyte activity and/or of neurohormonal release at the external vascular zone (Calas, 1975). Finally, the occurrence of occasional 5 HT axons reaching the parenchymal basement membrane suggests a true neurohormonal function for 5 HT. Moreover, a direct effect of 5 HT has been observed in the duck upon ACTH release (Calas, unpublished data).

Peptidergic innervation

LH-RH immunoreactivity was exhibited by varicose fibers in the external region of the rostral and caudal ME and also in the OVLT (Calas et al., 1973; Calas, 1975). These results have been confirmed by more recent investigations which demonstrated LH-RH immunoreactive perikarya in the arcuate (McNeill et al., 1976) and preoptic nuclei (Oksche, 1978; Bons et al., 1978). In contrast, AVT immunoreactivity was located in the whole of the hypothalamo-posthypophyseal tract, including neuronal cell bodies in the anterior hypothalamus, the entire neural lobe (NL) and dense bundles of nerve fibers in the internal ME. Numerous immunoreactive fibers were also observed in the external rostral part of ME (Calas, 1975). In contrast, no AVT positive fibers were detected in the OVLT, only some immunoreactive perikarya occurring caudally, very close to the organ. Finally, in contrast with the observations of McNeill et al. (1976), no immunoreactivity was found in tanycytes. Thus, AVT immunoreactivity is superimposable with AF stainability in the duck. The same situation holds for quail and pigeons (unpublished). A similar concordance between AF and neurophysin reactivities was found by McNeill et al., (1976). Using differentially absorbed AS, Goossens et al. (1977) have confirmed the distribution of AVT fibers in several species of birds; in contrast to AVT, mesotocin axons were only found in the hypothalamo-posthypophyseal tract, the different axonal bundles probably issuing from distinct parts of the anterior hypothalamus (Goossens et al., 1977; Blähser & Simon, 1978; Bons et al., 1978).

At the electron microscope level and using two distinct immunocytochemical approaches somewhat different and complementary results for the ME were obtained.

The pre-embedding procedure allowed for the detection of well-contrasted positive reactions in the periphery of the sections but no reaction was observed in the internal organ due to poor penetration of the AS. Immunocytochemical staining affected primarily, but not exclusively, the neurosecretory granules, the membranes of which displayed a welldefined shape in spite of inconstant morphological preservation. Their approximative diameters were suggestive of different kinds of neurosecretory axons, reactive fibers containing granules of either 100, 120—160 or 160—200 nm diameter for both peptides. Immunocytochemical staining with the postembedding technique displayed three characteristics: 1) the reactions were similar to those described at the histological level and affected the ME as well as the NL where about 50% of axonal sections were reactive (indicating that in these conditions, our AS do not cross-react with mesotocin); 2) the reactive character was confined to neurosecretory granules; 3) the size of these immunoreactive granules was smaller than those measured following the pre-embedding technique. Their diameters were not precisely determined owing to the absence of osmic postfixation and a consequent lack of a well-shaped membrane. However, they were estimated to measure 60—90 nm for LH-RH axons and 60—120 nm for AVT axons some of which were occasionally found to be myelinated in the anterior internal ME. These results are in good agreement with those of PELLETIER et al. (1974) for LH-RH in rat ME, and those of VAN VOSSEL et al. (1976) for AVT in the frog's NL. Irrespective of the technique employed the wide spectrum of reactive granules makes questionable the validity of axonal classifications based on morphological criteria.

In conclusion, it appears that the classically described anatomical divisions of the ME and OVLT in the duck might be correlated with distinct physiological functions. The internal parts of both organs are rather undifferentiated hypothalamic regions with neurosecretory neurons synaptically innervated by NA and possibly 5 HT fibers (lateral OVLT). The external regions where LH-RH (ME, OVLT), AVT (rostral ME) and 5 HT (ME) are concentrated and probably released constitute the true neuroendocrine parts of these similarly organized circumventricular organs. The target structures of the LH-RH which may be released from the OVLT are not known nor the function of AVT in rostral ME. The vascular links between the rostral ME and the anterior lobe of adenohypophysis in the duck (ASSENMACHER & TIXIER-VIDAL, 1964) as well as ultrastructural results concerning CRF activity in rostral ME of pigeon (PECZELY & CALAS, 1970) might help to elucidate it. Studies directed to a better understanding of the role of different monoamines in neuroendocrine control mechanisms might take advantage of the apparent lack of tubero-infundibular DA system in birds. For example, an antagonist function of 5 HT and NA in photostimulated gonadal growth has been postulated in quail following selective neurochemical destructions of either the 5 HT or the NA fibers (CALAS, 1975) and an inhibitory effect of 5 HT upon testicular response to photostimulation has been recently confirmed in the same species (EL HALAWANI et al., 1978). Besides their sensitivity to photoperiodic changes, birds might also be suitable for studying the complex problems of monoaminergic and peptidergic interrelationships in neuroendocrine regulations.

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Morphology and Function of the Subfornical Organ of the Circumventricular System in Relation to Drinking Behavior

Hideshi Kobayashi

Introduction

There are several morphologically specialized areas located in the ventricular system along the midline of the brain which together make up the circumventricular organs (see Weindl, 1973) (Fig. 1). Although these areas seem to be associated with neuroendocrine structures, their functions have not been well elucidated, except for those of the neural lobe, the median eminence and the pineal gland. In this paper, the morphology and function of the subfornical organ (SFO) of the Japanese Quail will be described briefly in relationship to angiotensin-induced drinking.

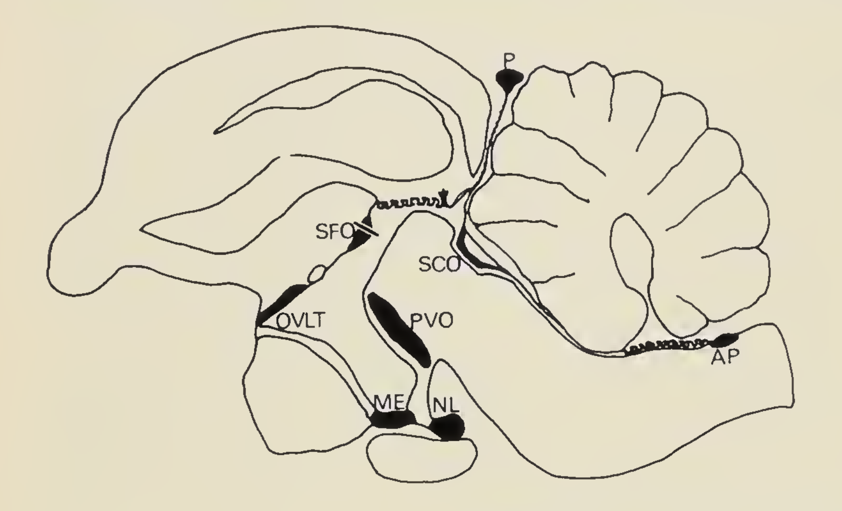


Figure 1. The circumventricular organs of birds. AP area postrema; ME median eminence; NL nerual lobe; OVLT organum vasculosum laminae terminalis; P pineal body; PVO paraventricular organ; SCO subcommissural organ; SFO subfornical organ.

Surface structure of the SFO

The small, ovoidal SFO of the Japanese Quail protrudes from the ventricular surface and is located on the rostral wall of the third ventricle, between the anterior commissure and the base of the choroid plexus (Fig. 1). It consists of a body and stalk, the body being divisible into rostral and caudal areas. In the rostral area, each ependymal cell possesses many microvilli and a short single cilium in the center. Occasionally, however, clustered cilia may be seen. In the caudal area, ependymal cells with a single cilium are fewer in number, microvilli are not abundant and clustered cilia are rarely found. In both parts, other surface structures, such as funnel-shaped cavities and large bulbous protrusions, are rarely seen. The contents of the protrusion seem to be discharged into the ventricle, the physiological significance of this phenomenon not yet being understood. Although supraependymal cell bodies are not found, long thin fibers, reminiscent of supraependymal axons, are occasionally observed on the ependymal surface of the rostral area of the body. No CSF-contacting neurons are encountered and the ependymal cells of the stalk have no clustered cilia. Cells with a single central cilium and those with abundant microvilli are few in number and other structures which may be seen in the body are also very rare in the stalk.

Co-authors: Joshio Takei and Kazuhizo Tsuneki
Author's address: Misaki Marine Station, University of Tokyo, Misaki, Miura-shi, Kanagawa-ken, 238—02, Japan

Parenchymal structure of the SFO

The SFO consists of ependymal, intermediate and basal (perimeningeal) layers (Fig. 2). In the intermediate layer, neurons, glial cells and various processes are present as well as many axons containing dense-cored granules (80 nm in diameter). Synapses are occasionally observed between these axons and the neuronal perikarya or dendrites. After treatment with 5-hydroxydopamine (5-OHDA), a dense core appears in the center of synaptic vesicles in some of these axons. From these observations it may be concluded that there are afferent monoaminergic (perhaps noradrenergic) axons in the SFO. In addition to these axons, there are a few which contain larger granules (120 nm in diameter) as well as synaptic vesicles. After treatment with 5-OHDA, the vesicles of the second axon type likewise show a dense core and, therefore, may also be monoaminergic. Cytoplasmic vacuoles of varying sizes are frequently observed but it is difficult to tell whether the cells with these vacuoles are glial or nerve cells. Endothelial cells of the capillaries in the intermediate layer of the SFO show no fenestration.



Figure 2. Diagram of a section of the subfornical organ (SFO) of the Japanese Quail. The site of the cut is shown in Figure 1. BL basal (perimeningeal) layer; C capillary; EL ependymal layer; G glial cells; H hollow-shaped cavity; IL intermediate layer; MV meningeal vessel; N neuron; P bulbous protrusion; T tanycyte; V cytoplasmic vacuole.

The basal layer is occupied by glial processes abutting onto the digitations of the perivascular connective tissue space of the meningeal vessel. This vessel looks like a sinus and a fenestrated endothelium is occasionally observed. The SFO is outside the blood-brain barrier as revealed by trypan-blue injection. Tanycytes are sometimes encountered. Neither fibers nor cell bodies which stain with paraldehydefuchsin are found.

Afferent monoaminergic fibers in the SFO

Fluorescence microscopy has revealed that monoaminergic fibers (perhaps noradrenergic) project from the preoptic area (POA) to the SFO and there are also fluorescent perikarya in the POA. Some of the monoaminergic fibers containing granules of 80—120 nm in diameter which are observed in the electron microscope may have their origin in the POA. There is no information about efferent nerve fibers.

Drinking behavior induced by Angiotensin II

Birds generally respond to intraperitoneally injected 5-valine angiotensin II (AII) by drinking (Table 1). It is interesting to note, however, that birds native to arid regions are relatively insensitive to AII, possibly dipsogenic receptors for AII may have decreased in number or affinity. The green Budgerigar, *Melopsittacus undulatus* (wild type), which is a native of the arid areas of Australia, is rather insensitive, whereas the yellow form, produced by artificial selection, is more sensitive. Possibly the yellow form has reaquired dipsogenic receptors for AII. Carnivorous birds, which ingest water

TABLE 1: Drinking induced by Angiotensin II (Asn^1-Val^5 AII) injected intraperitoneally

Species	number of birds	approximate minimum effective dose (m.e.d.) (μg/100 g BW)	largest number of pecks induced by m.e.d.	shortest latent period to m.e.d. (min)
Streptopelia risoria	4	1	9	3
Vanellus indicus	3	5	*	7
Zonotrichia leucophrys gambelii	5	5	13	2
Lorius lory	6	5	25	1
Acridotheres tristis	8	5	5	14
Passer montanus	2	5	6	5
Coturnix coturnix japonica	6	10	13	4
Psittacula krameri	8	10	7	3
Melpostes cafer	8	10	4	2
Emberiza bruniceps	6	10	6	1
Emberiza aureola ornata	5	30	12	1
Lonchura punctulata	4	1	2	8
Lonchura malacca	10	1	9	8
Lonchura malabarica[1]	4	no response even to 10 μg		
Melopsittacus undulatus				
green form[2]	6	100	15	1
yellow form	5	10	5	1
Falco tinnunculus[3]	5	1 000	34	17
Accipiter badius[3]	8	no response even to 1,000 μg		
Athene brama[3]	6	no response even to 1,000 μg		

* This water bird used its long beak like a straw and sucked the water.

[1] This species of *Lonchura* lives in arid areas in India and did not respond to even 10 μg of AII.

[2] Originated in arid regions in Australia.

[3] Carnivorous birds.

primarily from meat, are also insensitive to AII. It may be seen, therefore, that the birds which drink only a little water in the wild are insensitive to AII. However, there is no difference in the histological features of the SFO between the birds that are sensitive to AII and those that are not. It seems that the angiotensin-thirst mechanism has evolved adaptively in the physiological mechanisms that control thirst.

Function of the SFO in relation to drinking

Systemic and intracranial injections of AII induce drinking behavior in birds (Takei, 1977 a) and mammals (Epstein et al., 1970). When the SFO is lesioned by electric cautery, AII is no longer effective. This has been confirmed in the rat (Simpson & Routtenberg, 1973, 1975) and in the Japanese Quail (Takei, 1977 b). Injection of AII directly into the SFO does, however, induce drinking in the rat and the Japanese quail. Thus, it may be suggested that the SFO is possibly a receptive site for AII.

Epstein et al. (1970) first suggested, however, that the POA is the receptive site for AII in rats, and in the Japanese Quail injection of AII into the POA also induces drinking (Takei, 1977 a). The question therefore arises as to the location of the true AII receptor. Johnson & Epstein (1975) showed that AII, injected into the POA, leaks into the ventricle and perhaps reaches the SFO. However, Kucharczyk et al. (1976) suggest that neurons in both the SFO and the POA are receptive to AII and function independently in AII-induced drinking. Considering our data together with these findings, it seems that both the SFO and the POA are receptive sites for AII in mammals and birds.

We have primarily investigated the SFO and have shown by electron microscopy that it contains neurons which may possess receptors for AII. These neurons must perceive AII and send signals to higher centers involved in thirst regulation. It is assumed that AII, injected intravenously or intraperitoneally, may reach the neurons in the SFO. The facts that the meningeal vessels have a fenestrated endothelium and the perivascular connective tissue projects many digitations in the parenchyma support our idea and we have also shown that the blood vessels in the SFO are outside the blood-brain barrier. The intraventricularly-injected AII may reach the neurons in the SFO, which are located in the subependymal region, through the intercellular spaces and the funnel-shaped cavities may also facilitate the penetration of AII from the ventricular fluid into the parenchyma.

As mentioned above, the POA is also considered to be a receptive site for AII. What, then, is the functional relationship between the SFO and the POA? At the present time, we think that monoaminergic neurons located in the POA perceive the AII and transfer the information to the SFO. This information may be transported from the SFO to the higher centers involved in drinking. Evidence for this hypothesis is that 1) when monoaminergic fiber connections between the POA and the SFO are transected by a Halász-type knife in the Japanese Quail, drinking induced by AII injected into the POA is prevented and 2) noradrenalin injections into the SFO invariably induce drinking in the same birds. However, further suggestion is that changes in the structure of the periventricular vessels caused by AII may be signals for the induction of drinking behavior (Nicolaïdis & Fitzsimons, 1975). Further studies are needed to determine the exact sites responsible for drinking induced by AII.

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Photoreception and the Neuroendocrine Mechanisms Involved in the Photosexual Reflex in Birds.

J. D. Baylé

Introduction

The stimulating influence of light on testicular activity was first shown in the starling by Bissonnette (1931). Thereafter, Benoit (1934) demonstrated that ducklings submitted to 15 hr daily of artificial light for 3 weeks showed marked growth of the testes and since then a photosexual reflex has been observed in numerous avian species. Photoperiodic stimuli result in a logarithmic rate of growth of the testes (Follett & Farner, 1966) as well as in rapid increases in plasma levels of testosterone (Jallageas & Attal, 1968), LH (Nicholls et al., 1973) and FSH (Follett, 1976). Benoit's pioneering experiments (1936) showed both that the hypothalamus is stimulated by the eyes and also directly by light reaching the tissues. In turn, the hypothalamus stimulates the pituitary gonadotropic function. This report will deal with the neuroendocrine mechanisms and the photoreceptive activities which are involved in the photosexual reflex, as well as with their electrophysiological correlates.

Neuroendocrine mechanisms

Adenohypophysectomy prevents growth of the testes in ducks (Benoit, 1936) and in other species (Baylé, 1968). The hypothalamic adenohypophysial link is of primary importance in photostimulation of the gonads : transection of the portal veins (Assenmacher & Benoit, 1953) or ectopic pituitary autografts (Ma & Nalbandov, 1963;

Table 1: Effect of electrolytic lesions of the infundibular or preoptic areas on the pituitary-testicular axis in photostimulated quail (18 L:6 D)

Group (n)	Testicular wt	Plasma Testosterone (ng/10 ml)	Plasma LH (ng/ml)
Control (4)	3,240 ± 360	24.3 ± 3.7	4.48 ± 0.67
Infundibular lesions (6)	21.8 ± 3.3[a]	1.91 ± 0.49[a]	0.51 ± 0.05[a]
Preoptic lesions (4)	56.1 ± 13.0[a]	1.43 ± 0.23[a]	0.72 ± 0.13[a]

([a]: $p < 0.01$ vs control)

Assenmacher & Baylé, 1964) leading to gonadotropic quiescence. Destruction of the median eminence (Benoit & Assenmacher, 1952) inhibits gonadal activity. Electrolytic lesions of the infundibular complex suppress the photosexual reflex in quail (Sharp & Follett, 1969; Liver, 1972), pigeons (Bouillé & Baylé, 1973), sparrows (Wilson, 1967) and cockerels (Graber et al, 1967), Another area, located in the preoptic-ante-

Co-authors: J. Oliver and S. Herbuté

Author's address: Laboratoire de Neuroendocrinologie B., Département de Physiologie, Université de Montpellier II, France.

rior hypothalamic region, appears to intervene in the photosexual reflex (duck: ASSENMACHER, 1957; quail: OLIVER, 1972; pigeon: BOUILLÉ & BAYLÉ, 1973).

This situation was demonstrated recently in our laboratory (OLIVER et al., 1978 b; Table 1).

The reverse situation was observed in quail where a strong rise in LH level followed electrical stimulation of either the tuberal hypothalamus or the preoptic region (DAVIES & FOLLETT, 1975).

Photoreceptive activities

Numerous experiments have been undertaken in ducks in order to show that the eyes are involved in the gonadotropic response to light. Testicular growth was found to be significantly grater in intact than in blinded birds submitted to feeble illumination (BENOIT et al., 1953). The photosexual retina is very sensitive to orange and red rays and insensitive to yellow, green and indigo rays, whereas the visual retina has maximum sensitivity to yellow light. The eyes may also be involved in the photoperiodic regulation of gonadotropic activity in Coturnix quail (HOMMA et al., 1972). Photostimulated (18 $L_{5\,lux}$: 6 D) intact quail have a significantly higher (X2) testicular weight than have blinded birds (BONS et al., 1975). Retinal hypothalamic connections have now been demonstrated in birds. Degenerating fibers and presynaptic profiles were seen in the anterior hypothalamus after optic nerve section in ducks (BONS & ASSENMACHER, 1969) while direct retinal afferents to the hypothalamus have been observed in chickens, sparrows, pigeons and jackdaws (for references, see OLIVER et al., 1978 a). Ganglion cells projecting to the hypothalamus have been visualized in the retina of quail (OLIVER et al., 1978 a).

Horseradish peroxidase was injected into the preoptic-anterior hypothalamic area. Thirty hours later the head was perfused and sections of the eyeball reacted with 3,3' -diaminobenzidine and hydrozen peroxide. Scattered cells labelled by retrograde transport of protein were observed in the ganglion layer of the retina. However, blinding does not prevent light stimulating testicular growth in ducks (BENOIT, 1935) and in quail (OLIVER & BAYLÉ, 1973). The eyes are not necessary for photoperiodic induction of gonadal growth in chickens, quail and sparrows (for references, see MENAKER & KEATTS, 1968). Hence, deep photoreception does occur and leads to gonadotropic activation. As early as 1937 BENOIT reported that light applied directly to the hypothalamus by a quartz rod exerts a strong effect on testicular growth. Optic fibers, 0.3 mm in diameter, implanted in the hypothalamus, led to positive responses when light was directed straight into the infundibular complex. Illumination of the brain using radioluminous material (RLM) maintained large testes in birds when they were transferred to short days (KATO et al., 1967). Application of RLM on the skull (FOLLETT et al., 1974), or along the fissura longitudinalis cerebri (HOMMA & SAKAKIBARA, 1971), resulted in as much testicular growth as was found in birds exposed to long daylengths.

Implantation of small (0.6 × 0.2 mm) pellets of RLM allowed selective photostimulation of various parts of the hypothalamus (OLIVER & BAYLÉ, 1976 a). Local lighting of the infundibular complex leads to significant enlargement in quail reared under short days, even after neural deafferentation (DAF) of the basal hypothalamus (OLIVER et al.,

TABLE 2: Effect of radioluminous stimulation (RL) of the infundibular complex (IC) or the anterior-preoptic area (POA)

Group (n)	Control (9)	RL/IC (13)	RL/IC DAF (5)	RL/POA (8)	Control (14)
Photoperiod	18 L:6 D	6 L:18 D	6 L:18 D	6 L:18 D	6 L:18 D
Testes wt (mg)	1,839 ± 234[a]	1,841 ± 323[a]	1,423 ± 223[a]	78 ± 21	72 ± 14

([a]: $p < 0.01$ vs non-photostimulated controls)

1977: Table 2). In contrast, local photostimulation of the preoptic-anterior hypothalamic region never induces a photosexual response.

Plasma levels of testosterone and LH are also significantly increased after infundibular RLM photostimulation but preoptic placement of the pellet was ineffective (OLIVER et al., 1978 b: Table 3).

TABLE 3: Plasma levels of testosterone and LH after RLM implantation in the infundibular complex (IC) or preoptic area (POA)

Group (n) (6 L:18 D)	Testosterone (ng/10 ml)	LH (ng/ml)
Control (6)	0.72 ± 0.03	0.38 ± 0.01
RLM/IC (6)	23.0 ± 1.3[a]	3.87 ± 0.41[a]
RLM/POA (3)	1.45 ± 0.66	0.94 ± 0.25

([a]: $p < 0.01$ vs Control)

Extraretinal photosensitivity was also described in central nervous structures such as the rhinencephalic region (BENOIT & KEHL, 1939). OISHI & KATO (1968) noted that illumination of the pineal stimulated the growth of the testes in quail. Pinealectomy of sparrows inhibited the circadian rhythm of locomotor activity, but the pineal was found not to be necessary for the entrainment of photoperiodically stimulated testicular growth (MENAKER et al., 1970). MORITA (1966) and RALPH & DAWSON (1968) found no correlation between pineal electrical activity and light. However, recording the pineal multiunit activity (MUA) from unanaesthetized quail indicates that light influences pineal MUA (Table 4).

TABLE 4: Effect of light on pineal MUA in intact (I), blinded (ON), ganglionectomized (GGL) and habenulectomized (Hb) quail

Group (n)	Photoperiod	Spontaneous MUA (200 sec)	Flash-altered MUA (200 sec)
I (30)	6 L:18 D	1,004 ± 129	621 ± 80[b]
I (19)	18 L: 6 D	504 ± 42[a]	283 ± 21[b]
ON (42)	6 L:18 D	2,210 ± 174	2,157 ± 162
ON (15)	18 L: 6 D	1,899 ± 267	1,801 ± 222
GGL (36)	6 L: 18 D	1,460 ± 75	1,012 ± 58[b]
GGL (21)	18 L: 6 D	635 ± 56[a]	403 ± 50[b]
Hb (8)	6 L:18 D	1,298 ± 60	1,259 ± 71
Hb (10)	18 L: 6 D	692 ± 16[a]	679 ± 16

([a]: $p < 0.01$ vs non photostimulated birds; [b]: $p < 0.01$ vs spontaneous MUA)

Flash stimulations induce a marked decrease in pineal activity in intact quail (Herbuté & Baylé, 1974) and this inhibitory effect of acute lighting continues after ganglionectomy but disappears after optic nerve section or habenulectomy (Herbuté & Baylé, 1976). Pineal firing rates are lower in photostimulated birds than in non photostimulated ones except for those that had been blinded. The effects of light on pineal MUA appear therefore to be mediated through retinal information and partly via habenular pathways (Herbuté & Baylé, 1977).

Hypothalamic electrophysiological correlates

Flash-evoked potentials were recorded in unanaesthetized quail from infundibular regions where lesions suppress the photosexual reflex (Oliver & Baylé, 1973). Infundibular responses to flash-lights are characteristic and homogeneous. Their latency is longer than in the optic chiasma and shorter than in other hypothalamic areas (Table 5). Changing the lighting pattern from 6 L : 18 D to 18 L : 6 D shortens the latency but testosterone treatment has the same effect.

Table 5: Latency (msec) of flash evoked potentials

	Site of record		
	Optic chiasma	Infundibular complex	Non gonadotropic area
6 L: 18 D (n)	7.6 ± 0.7 (34)	14.3 ± 0.4 (91)	18 ± 1
18 L: 6 D (n)	7.5 ± 0.8 (12)	12.3 ± 0.5[a] (24)	18 ± 1

Multiunit activity (MUA) was obtained from neuronal pools in the same hypothalamic regions in birds which were resting but awake. Spontaneous firing rates are higher during the light than during the dark part of a short photoperiod but flash stimulations result in a significant although slow increase in MUA (Oliver & Baylé, 1975: Table 6). Spontaneous infundibular MUA is markedly decreased and flash-induced activation is suppressed after blinding.

However, daily variations of discharges do not disappear after optic nerve section. Lengthening the daily photoperiods from 6 L : 18 D to 18 L : 6 D causes a marked reduction in firing rates and flash stimulations are no longer effective.

Table 6: Infundibular MUA (spikes/200 sec)

Group (n)	Photo-period	Mean Spontaneous MUA	Light period	Dark period	Flash-altered
Intact (97)					
Blinded (92)	6 L: 18 D	468 ± 95	546 ± 94	292 ± 68[c]	935 ± 142[b]
Intact (88)	6 L: 18 D	286 ± 39[a]	319 ± 35	215 ± 26[c]	294 ± 49
	18 L: 6 D	206 ± 24[a]	—	—	196 ± 27

([a]: $p<0.01$ vs intact 6 L: 18 D; [b]: $p<0.01$ vs spontaneous; [c]: $p<0.01$ dark vs light)

Similar results were obtained after local illumination (by means of RLM) of the infundibular complex (Oliver & Baylé, 1976 b) when spontaneous MUA is decreased (265 vs 341 spikes/200 sec in controls) and the post-flash activation is suppressed (208 spikes/200 sec). At least, neither a systematic MUA increment after flash-lighting nor variations because of changed daily photoperiods can be observed in non-gonadotropic regions of the hypothalamus of intact quail.

Table 7: Preoptic MUA (spikes/200 msec)

Group (n)		Photoperiod	Spontaneous MUA	Flash-altered MUA
Intact	(4)	6 L: 18 D	532 ± 24	425 ± 22[b]
	(4)	18 L: 6 D	215 ± 16[a]	140 ± 10[b]
Blinded	(4)	6 L: 18 D	278 ± 35[a]	265 ± 31
	(4)	18 L: 6 D	221 ± 15[a]	209 ± 14

([a]: $p < 0.01$ vs intact 6 L: 18 D; [b]: $p < 0.01$ vs spontaneous)

Spontaneous preoptic MUA (Oliver & Baylé, 1977) is lower in photostimulated than in quiescent birds (Table 7). Flash stimulations provoke an early (few msec) and significant (× 6) peak in firing rates. Thereafter, MUA is low for approx. 250 msec. Somewhat similar responses to flashes may be observed in the optic tectum but blinding results in decreased preoptic spontaneous discharges and suppression of flash-induced activity.

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Gonadotrophin Secretion in Seasonally Breeding Birds and its Control by Daylength

B. K. Follett

Introduction

Birds have evolved a bewildering array of ecological and ethological adaptations for breeding, the aim of which is to assist each species to produce as many offspring as possible and to maximise the chances of these offspring reaching sexual maturity. It is this selective pressure which has led to developments such as seasonal breeding, to migration into higher latitudes, to sophisticated patterns of sexual behaviour, and probably also to phenomena like deferred maturity. Although many of these adaptations operate ecologically they all depend upon underlying physiological adaptations, and in a number of cases (e.g. yolk deposition and hence clutch size, migration, secondary sex characters and behaviour) are controlled by the appropriately timed secretion of various hormones. As an endocrinologist rather than an ecologist my interests have concentrated on these underlying processes and upon one in particular: how exactly do proximate environmental factors such as daylenght trigger reproduction? The problem has been tackled in the laboratory using a "model" species: in our case the Japanese Quail *(Coturnix coturnix japonica)* (reviews: Follett, 1973 a, b, 1978; Follett & Davies, 1975; Davies & Follett, 1975; Davies et al., 1976). This has many advantages but it also has its limitations and the next stage is to apply the results to the field biology of wild species (e.g. Wingfield & Farner, 1978).

Much success has come from using radioimmunoassay methods which can measure the hormones in small (10—100 µl) samples of blood, thus giving an accurate picture of the endocrine situation. In the case of those hormones whose structure is similar in most vertebrates (e.g. the steroids, insulin, thyroxine) immunoassays can be adapted from methods devised for mammals, but this is not so possible for the pituitary hormones where species differences are substantial. So far, however, methods have been devised for LH (Follett et al., 1972; Wentworth et al., 1976), FSH (Croix et al., 1974; Follett, 1976; Scanes et al., 1977), prolactin (Scanes et al., 1976) and growth hormone (Harvey & Scanes, 1976). All immunoassays are fraught with potential hazards and validation is a serious problem (review, Follett et al., 1978). Bird plasma has characteristics different from that of mammals (e.g. vitellogenin in females, the binding affinities of the serum albumins) and this causes difficulties with steroid and thyroxine assays. Fortunately, the cross-reaction of the protein hormone assays has generally been found to be quite wide and the chicken LH system, for example, has been used with members of the Galliformes, Anseriformes, Charadriiformes, Columbiformes and Passeriformes. For FSH the situation is less satisfactory as few materials are available, while for prolactin some debate still rages about the validity of the assays. The functions of the various hormones in birds do not appear to depart radically from those in mammals.

Department of Zoology, The University, Woodland Road, Bristol BS8 1UG, United Kingdom.

The photoperiodic control of gonadotrophin secretion in birds

On transferring quail from short (8 L: 16 D) to long (20 L:4 D) daylengths plasma FSH and LH levels rise within 24 h and peak secretion occurs after 7—10 long days (Figure 1). This causes a rapid phase of gonadal growth which in the testis comes about both from spermatogonial division, leading to an increase in tubule diameter, and from growth in tubule length. After 15 days, however, at the time when the Sertoli cells are fully differentiated and becoming associated with the maturing spermatids, there is a rapid decrease in FSH secretion to about 100 ng/ml (Figure 1) and the rate of testicular growth slows ten-fold. A similar pattern of FSH secretion occurs during ovarian growth but in neither case is it clear what agents cause the fall in FSH as the gonads mature. The pattern of LH secretion under 20 L:4 D is slightly different (Figure 1). The level remains relatively stable once it is elevated, and it is unchanged into maturity. LH first stimulates differentiation of the Leydig cells and then androgen secretion. In turn, the androgens cause growth of the secondary sex characters and development of sexual behaviour which starts to become apparent after 10—14 long days.

The rate of gonadal growth in birds is proportional to daylength once it exceeds a critical duration, and this is due to an effect of daylength on FSH secretion (Follett & Maung, 1978). As Figure 1 illustrates there is no peak of FSH secretion in quail expo-

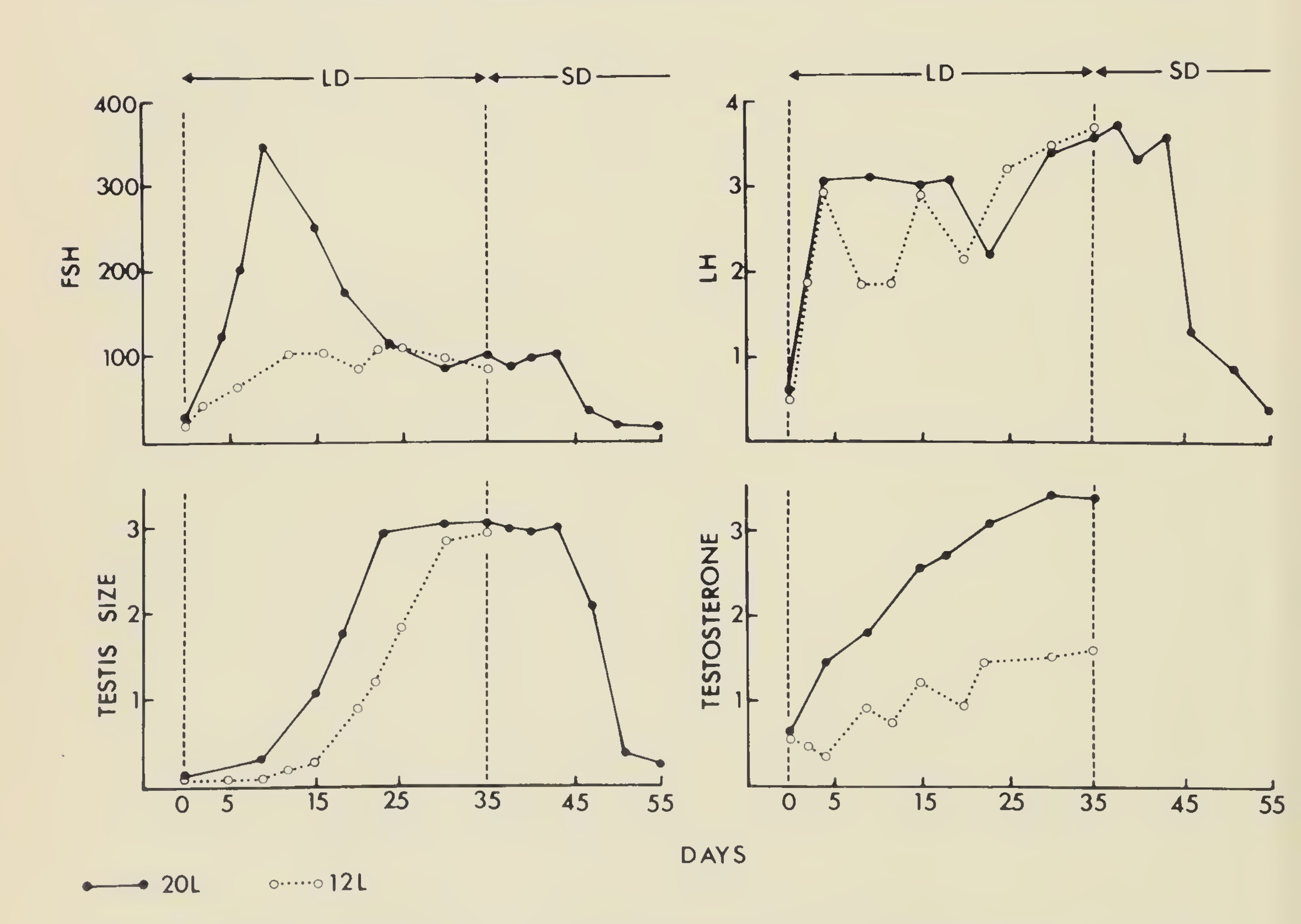


Figure 1. Changes in testicular size and plasma levels of FSH, LH and testosterone in male Japanese Quail transferred at day O from short daylengths (SD, 8 L: 16 D) to long photoperiods (LD) of either 12 L: 12 D (O) or 20 L: 4 D (●). After 35 days quail under 20 L: 4 D were transferred back to 8 L: 16 D to induce testicular regression. For the sake of clarity errors around each mean have been omitted. From Follett (1976, 1978) and Follett & Maung (1978).

sed to 12 L: 12 D and testicular growth is slowed by about 50 %. Interestingly, there is no difference between the output of LH on 12 L: 12 D and 20 L: 4 D, perhaps reflecting slightly different photoperiodic thresholds for the two gonadotrophins. Since, however, testosterone secretion is less on 12 L: 12 D one suspects that FSH (or perhaps prolactin or TSH) may have an indirect action on the interstitium's ability to respond to LH, a phenomenon known in mammals.

The rise in LH and FSH secretion at about hour 18 on the first long day (regardless of its length, FOLLETT et al., 1977) emphasises the speed of the photoperiodic response, and argues that however the bird's circadian system is involved in measuring daylength it exhibits little lag, and can be triggered merely by exposing a quail to 4 hours of light placed 12 to 16 hours after dawn. In some birds (Figure 2) a further rise in LH secre-

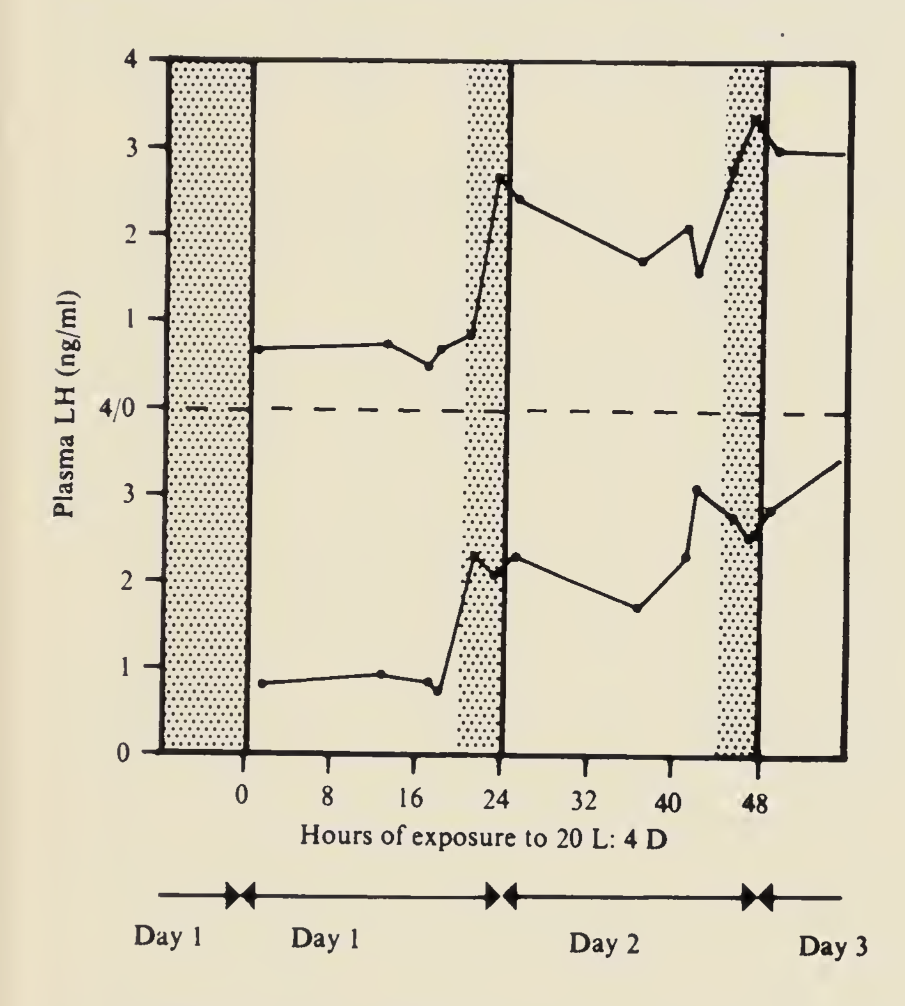


FIGURE 2. Plasma LH levels in two male quail during the first two days of exposure to 20 L: 4 D (darkness is shown by shading). Note the rises late in the photoperiod on each day. From FOLLETT et al. (1977).

tion occurs at an equivalent time on the second long day, just as if it was at this point that the bird's circadian clock "decided" it was a long day, but such rhythmicity is soon lost and there is no further pronounced diurnal secretion of LH or FSH (GLEDHILL & FOLLETT, 1976, see also BALTHAZART et al., 1977). A hint as to why this occurs comes from observations on the effect of transferring birds back from long to short daylengths (or to darkness). Rather unexpectedly (Figure 1), the levels of LH and FSH do not fall away immediately but remain high for a week or so before decreasing. Since hypothalamic deafferentation causes an immediate fall in LH (DAVIES & FOLLETT, 1975) carry-over would appear to be a hypothalamic phenomenon, and to be a characteristic property of the photoneuroendocrine machinery. It would seem, therefore, that long days, measured by some circadian-based clock which is rhythmic in function (FOLLETT, 1973 b, 1978), are converted by a neural circuit into the continuous output of LH-RH from the hypothalamus. The nature of the circuit remains speculative but at

whatever level it exists, it has the property of remaining switched "on" for a number of days, even in the absence of further inputs in the form of long days. It is probably the development of this semi-permanent switch which eventually obscures the daily rhythmicity in hormone output visible during the first few long days. The adaptive significance of such an arrangement may be to ensure a steady flow of gonadotrophin to the gonad rather than one which fluctuates wildly during the day and night.

In contrast with mammals episodic secretion is less marked in quail, and the enhanced output of LH under long days is due primarily to increased tonic secretion (Gledhill & Follett, 1976). This may be different from the situation in the Soay sheep (Lincoln et al., 1977) where short days are thought to act mainly by enhancing the frequency and amplitude of the LH secretory episodes, with only a relatively minor effect on tonic secretion. To determine the detailed changes in output would be valuable since they must represent events very close to the neural and neuroendocrine circuits discussed above.

The Quail is not a classic photorefractory species and will remain fully mature for up to three years when held on 20 L: 4 D. However, in those species which show refractoriness LH and FSH levels first rise on long days, just as in quail, but then decrease dramatically after 50—80 days and the testes collapse.

The photoperiodic response is normally damped by sex steroids. Exposure of castrates to long days, for example, leads to enormous increases with LH often reaching 100 ng/ml and FSH 2,000 ng/ml (c. f. Figure 1). Feedback resides at both the pituitary and the hypothalamus and there are small changes in sex steroid sensitivity during photostimulation (Davies et al., 1976). However, long days do not act in quail by simply altering the sensitivity of a "gonadostat" in the hypothalamus: gonadectomized quail are completely photoperiodic (Gibson et al., 1975). In other species, however, this possibility still exists and because such a change has been implicated in mammalian puberty (and an homology suggested beween puberty and the seasonal growth of the gonads) it remains of interest. Kordon & Gogan (1970) suggested that perhaps a sudden increase in sensitivity of the hypothalamus to sex steroids may explain the onset of refractoriness in ducks and this idea is supported by more recent work (Cusick & Wilson, 1972; Sharp & Moss, 1977). Unfortunately, castrated birds become refractory (Wilson & Follett, 1974; Mattocks et al., 1976) and this greatly complicates the hypothesis, forcing the suggestion that possibly adrenal steroids might be responsible for the feedback effects in castrates. Alternatively, the results with castrates can be viewed as rendering the feedback idea untenable, at least in any simple form. Recently, Karsch et al. (1978) have produced good evidence in sheep in favour of short days triggering LH secretion by altering feedback sensitivity and the concept is again in the forefront of discussion.

Hormone secretion under artificial long days appears generally similar in all those species which have been investigated (quail, turkey, Peking Duck, teal, canary, Tree Sparrow, White-crowned Sparrow, Starling) but to what extent does it reflect the situation under natural daylengths? Figure 3 shows changes in male quail living on the roof of the Department in Bangor. As expected, the first signs of gonadal growth occurred when the photoperiod (including civil twilight) exceeded 12 hours and the time to full maturity (40—50 days) agrees well with experimental rates of growth. There was no

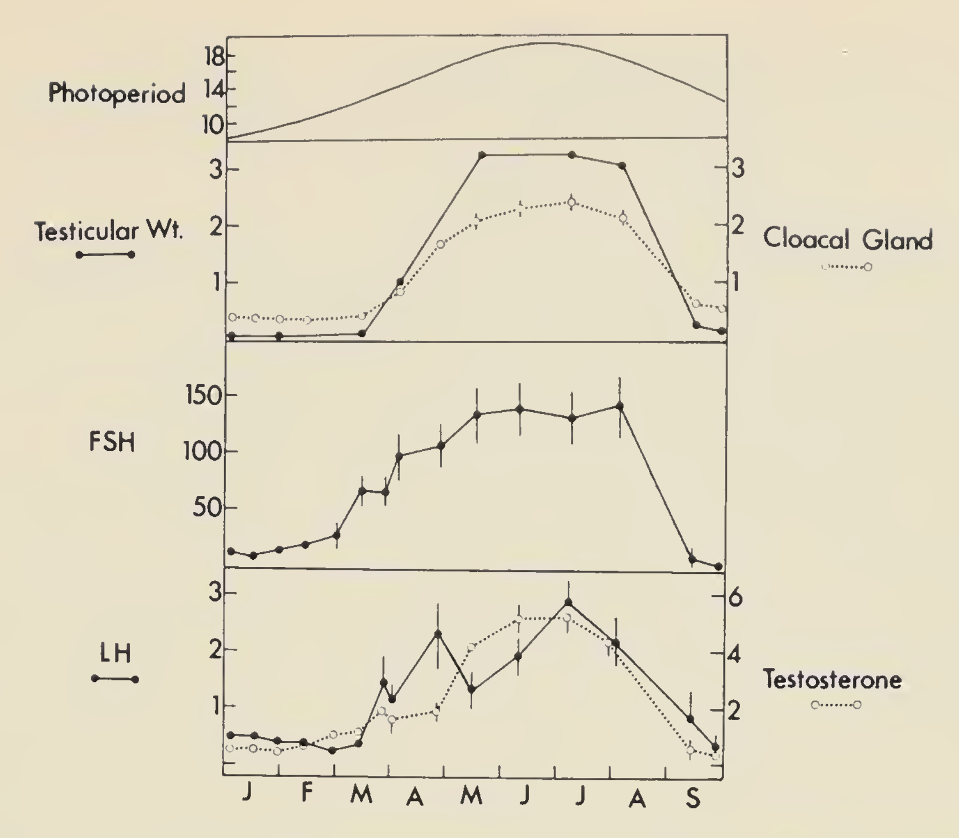


FIGURE 3. Testicular size (g), cloacal gland size ($mm^2 \times 10^{-2}$) and hormone secretion (ng/ml in vall cases) in a group (n = 12) of male quail exposed to natural daylengths during 1976. The uppermost panel shows the daylength (including civil twilight) at Bangor. Where appropriate the S.E.M. is shown. From FOLLETT & MAUNG (1978).

peak in FSH secretion, probably because by the time that the daylengths were long enough to stimulate maximal FSH secretion ($\geqslant$14 h) the testes had already reached 1500 mg in weight and inhibited high levels of FSH output. The birds remained in breeding from May to July but gonadal regression then began and the testes were completely regressed by early September when the photoperiod was still about 13 hours per day. Clearly, regression occurs under daylengths which in spring are maximally stimulatory. Since quail with regressing gonads in August could immediately be stimulated back into full reproduction by exposure to 18 L: 6 D (the longest day at Bangor) they were not "photorefractory" in the classic sense. This asymmetry within the breeding season seems to occur also in Californian Quail, some pigeons and the Baya Weaver Finch *Ploceus philippinus*. Possibly, however, its significance has been overlooked. How is it that a photoperiod containing 13 h causes growth in birds coming from short days but regression in quail coming from long days? The answers might influence some of our views on photoperiodic time-measurement!

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The Endocrine Control of Ovulation in Birds

P. J. Sharp

Introduction

At the beginning of the breeding season or at the onset of sexual maturation, ovarian follicles enter a final rapid growth phase during which yellow yolk is rapidly accumulated and steroids, particularly oestrogens and progesterone, are secreted in increasing amounts. This progressive development of ovarian follicles is reflected in a sequence of steroid-dependent behavioural changes—courtship, nest site selection, nest building and mating—which culminate in egg laying. In addition to acting on the brain to produce behavioural changes, the steroids produced by yellow yolky ovarian follicles also play an important part in the maturation and control of the neural mechanism which regulates the preovulatory release of luteinizing hormone (LH), the hormone responsible for the induction of ovulation. This paper reviews the roles of oestrogen and progesterone in the mechanism which ensures that the brain will stimulate a preovulatory release of LH when the ovary contains a mature follicle.

Maturational changes in the ovarian follicle before ovulation

The ovarian follicle becomes capable of ovulation between 4 and 11 days after the beginning of its final rapid growth phase. Studies on the quail and the hen show that up until about 48 hours before ovulation increasing quantities of oestrogens accumulate in the wall of the rapidly growing follicle (Kumagai & Homma, 1974; Shahabi et al., 1975). However, during the 24 hours before ovulation oestrogen production decreases and progesterone becomes the most important follicular steroid (Shahabi, et al., 1975). The follicle also becomes much more sensitive to the steroidogenic effects of LH during the 24 hours before ovulation (Etches & Cunningham, 1976 a). Thus, as the follicle becomes capable of ovulation, it secretes more progesterone in response to unchanged or even depressed (Sharp, 1976) base-line levels of plasma LH.

Variations in the concentrations of plasma oestrogens, progesterone and luteinizing hormone before ovulation

As birds come into lay the maturational changes occuring in the growing follicles are reflected in the levels of hormones in the blood. The onset of ovarian growth is associated with a steady increase in the levels of plasma LH and oestrogen but not of progesterone (Senior, 1974; Korenbrot et al., 1974; Silver et al., 1974; Sharp, 1975; Cheng & Follet, 1976; Williams & Sharp, 1977). The increasing level of plasma oestrogen is due to the presence of rapidly growing medium sized yellow yolky follicles while the concentration of plasma progesterone starts to increase only after the ovary contains a mature ovarian follicle. Thus the concentration of plasma progesterone, at the onset of lay, increases about a day before ovulation (Silver et al., 1974; Williams

Agricultural Research Council's Poultry Research Centre, King's Buildings, Edinburgh EH9 3JS, United Kingdom.

& SHARP, 1977). A high concentration of plasma progesterone is therefore a good marker for the presence of a mature ovarian follicle.

In the laying hen, the ovary usually contains a follicle which is within 24 hours of ovulation and consequently the level of plasma progesterone remains high. As the time approaches for a preovulatory surge of LH to be initiated (see below), increased secretion of progesterone by the mature follicle results in a small rise in the concentration of the steroid in the peripheral circulation (WILLIAMS & SHARP, 1978). In birds laying, on average, less than one egg every 24 hours it is likely that there will be larger daily variations in the level of plasma progesterone which depend upon the stage of maturation of the largest ovarian follicle.

LH stimulates the secretion of progesterone and oestrogen (SHAHABI et al., 1975) and it is not surprising that the preovulatory surge of plasma LH is accompanied by preovulatory surges of both steroids (FURR et al., 1973; LAGUË et al., 1975; SHODONO et al., 1975; TANABE, 1977).

The role of oestrogen and progesterone in the induction of the preovulatory release of luteinizing hormone

The observation that progesterone is the principal steroid produced by mature ovarian follicle suggests that the preovulatory release of LH is due to the ›positive feedback' action of progesterone rather than oestrogen (as in mammals) on the brain and pituitary gland (Fig. 1). This suggestion has been thoroughly investigated in the domestic hen and shown to be correct. Injection of progesterone, but not of oestrogen, in laying hens, or suitably primed (see below) ovariectomized hens, stimulates LH secre-

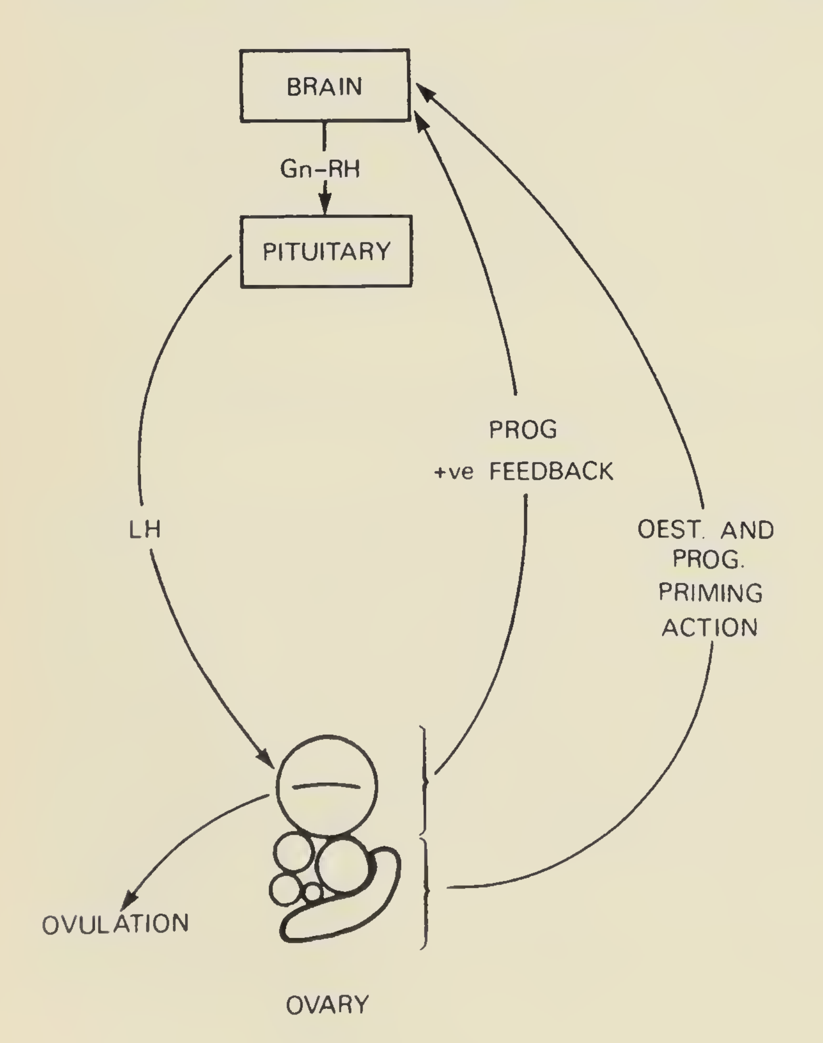


FIGURE 1. Diagram to illustrate the roles of oestrogen and progesterone in the control of ovulation. Progesterone secreted by the mature ovarian follicle stimulates an increased release of gonadotrophin releasing hormone (Gn-RH) from the brain by 'positive (+ve) feedback'. The increased release of Gn-RH stimulates the preovulatory release of luteinizing hormone (LH) from the pituitary gland which in turn stimulates further progesterone secretion. In this way the pre-ovulatory surge of LH, which causes ovulation, is built up. Before progesterone can induce LH release, the positive feedback mechanism must be first 'primed' for several days with oestrogen and progesterone secreted by developing ovarian follicles.

tion (Wilson & Sharp, 1975 a, 1976 a, b) while ovulation can be blocked by injection of anti-progesterone serum but not anti-oestradiolserum (Furr & Smith, 1975). Progesterone exerts its positive feedback effect on LH release by stimulating the secretion of gonadotrophin releasing hormone (Gn-RH) from the brain (Fig. 1) rather than by increasing the sensitivity of the pituitary gland to Gn-RH. This conclusion may be drawn from the observations that the sensitivity of the pituitary gland to synthetic LH-releasing hormone (LH-RH) does not increase before ovulation (Bonney et al., 1974) while the positive feedback action of progesterone on LH release can be blocked by an injection of anti-LH-RH serum (Fraser & Sharp, 1978).

The role of oestrogen and progesterone in the maturation of the positive feedback mechanism

Injection of progesterone will not stimulate LH release in juvenile hens (Wilson & Sharp, 1975 b), in adult hens with regressed ovaries (Sharp, unpubl.) or in ovariectomized hens (Wilson & Sharp, 1976 b). It therefore seems that the positive feedback mechanism must be 'primed' before it can be stimulated by progesterone. LH release is weakly stimulated in the hen by an injection of progesterone soon after the onset of sexual maturation but the full positive feedback response to progesterone is not observed until the largest ovarian follicle is mature (Wilson & Sharp, 1975 b). Since this weak positive feedback response occurs when the concentration of plasma oestrogen is increasing and the full response occurs after the level of plasma progesterone rises, it is likely that the positive feedback mechanism needs to be primed by a sequential exposure to oestrogen and oestrogen combined with progesterone (Fig. 1). This hypothesis was confirmed in ovariectomized hens in which it was found that LH release could be induced by an injection of progesterone provided the birds were primed for a week with a combination of injections of oestrogen and progesterone (Wilson & Sharp, 1976 b). If either steroid was removed from the priming schedule, LH release could not be stimulated by an injection of progesterone.

The timing of the preovulatory surge of LH

Ovulation and the preovulatory release of LH in the hen occurs only during a restricted period of the day (Fraps, 1955; Wilson & Sharp, 1973). From studies on egg laying patterns in hens exposed to ahemoral lighting cycles of between 21 and 30 hours (Biellier & Ostmann, 1960), it can be deduced that the timing of the preovulatory release of LH is probably determined by a circadian rhythm which is entrained by the anticipated onset of darkness. It is not known whether the pattern of ovulation observed in the hen occurs generally in other birds. Indeed, some Japanese Quail do not lay eggs during a restricted period of the day but lay 'around the clock' (Planck & Johnson, 1975). The neuroendocrine basis of the mechanism timing the occurrence of preovulatory surges of LH in the hen is not fully understood. Fraps (1955) suggested that it might be due to an increase in the sensitivity of the positive feedback mechanism for an 8 hour period every 24 hours. Attempts to demonstrate such a change in sensitivity have failed (Wilson & Sharp, 1975 a; Etches & Cunningham, 1976 a). Another suggestion is based on the observations that corticosterone injections will stimulate the release of LH and induce ovulation in laying hens (Etches & Cunningham, 1976 b;

Sharp & Beuving, 1978) and that there is a daily rhythm of plasma corticosterone secretion in hens (Beuving & Vonder, 1977). A nocturnal increase in the concentration of plasma corticosterone could trigger preovulatory releases of LH. The principle objection to this hypothesis is that the amount of corticosterone needed to induce LH release is well above the physiological range (Sharp & Beuving, 1978).

A hypothesis currently under investigation is that the timing of the preovulatory release of LH depends on a diurnal rhythm in the concentration of base-line plasma LH (Williams & Sharp, 1978). A nocturnal increase in the concentration of base-line plasma LH has been demonstrated in juvenile chickens (Scanes, et al., 1978). It is proposed that a nocturnal increase in the level of plasma LH stimulates the maturing ovarian follicle to secrete progesterone: the amount of progesterone secreted is directly related to the maturity of the follicle. If the largest ovarian follicle is fully mature, then the nocturnal increase in plasma LH will stimulate the secretion of a quantity of progesterone sufficient to trigger the positive feedback mechanism and cause a preovulatory surge of LH.

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SYMPOSIUM ON OSMOREGULATION IN BIRDS

7. VI. 1978

CONVENER: ERIK SKADHAUGE

Central Components and Input Factors in the Control of Salt Gland Activity

E. SIMON, H. T. HAMMEL and CHRISTA SIMON-OPPERMANN

Striking differences between the autonomic control functions of the rostral brain stem in mammals and birds have been revealed by comparative studies on its role in temperature regulation (SIMON, 1977). The avian hypothalamus lacks a significant thermoreceptivity as it is typical for mammals and exhibits a non-thermoregulatory temperature dependence (for references see SIMON-OPPERMANN et al., 1978 b). These findings have posed the question to what degree do non-thermoregulatory control functions of the rostral brain stem in birds deviate from those in mammals. With regard to osmoregulation, the analysis of this question has to consider a particular effector system, the supraorbital salt glands, which exist in many birds but not in mammals. While the control of renal excretion by hypothalamo-hypophyseal hormones establishes a close functional link between the rostral brain stem and osmoregulation, both in birds and mammals, little is known about receptive, integrative and efferent functions of this brain stem section relating to salt gland activity.

Central components in salt gland control

After the discovery of osmoregulatory functions of the avian supraorbital salt glands by SCHMIDT-NIELSEN et al. (1957), it was assumed that their activity was controlled by brain stem osmoreceptors as they exist in mammals (SCHMIDT-NIELSEN, 1960). However, according to HANWELL et al. (1972) evidence for brain stem osmoreceptors is lacking in birds. These authors have furthermore shown that the salt glands could be activated by osmotic stimuli even in the decerebrated goose. Thus, it might be questioned, whether the hypothalamus was involved at all in the control of salt gland function. A negative answer would be not too surprising in view of the independent evolution of the renal and salt gland osmoregulatory mechanisms.

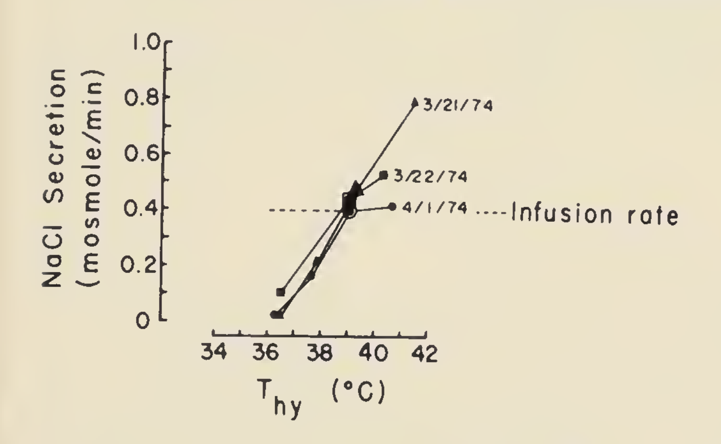


FIGURE 1. Relationship between salt gland secretion and hypothalamic temperature in an Adelie Penguin during 30 min of displacements of hypothalamic temperature from its normal value (39 °C) by means of chronically implanted water-perfused thermodes. The animal received a steady osmotic load of 0.4 mosm · min^{-1} by intravenous infusion of a 1 molar NaCl solution (HAMMEL et al., 1977).

However, observations of HAMMEL et al. (1976; 1977) indicate that the hypothalamus is somehow involved in the control of salt gland function. As shown by Fig. 1, local changes of hypothalamic temperature clearly influenced the Adelie penguin's salt gland activity, when the animal secreted under a steady salt load by intravenous infusion of hypertonic NaCl solution. These findings were confirmed by experiments in salt

Co-author: H. DEUTSCH
First author's address: Max-Planck-Institut für Physiologische und Klinische Forschung, W. G. Kerckhoff-Institut, D-6350 Bad Nauheim, Bundesrepublik Deutschland.

adapted Peking ducks in which hypothalamic cooling reduced salt gland activity. Obviously hypothalamic nervous mechanisms exist which relate to salt gland activity. Their temperature dependence is similar to that found for the thermoregulatory mechanisms located in the same region. This refers also to the hypothalamic control of renal water excretion: Hypothalamic cooling in ducks induced water diuresis due to inhibition of ADH release (SIMON-OPPERMANN et al., 1976).

The apparently identical effects of local hypothalamic cooling on both renal and salt gland function suggest that the hypothalamus forms a central link between these phylogenetically independent osmoregulatory effector systems. Thus, a precondition seems to be fulfilled for an eventually positive answer to the question posed by PEAKER & LINZELL (1975): Does the kidney know when the salt glands are switched on and vice versa?

The mechanisms by which hypothalamic integration of salt gland and kidney function might be established have not yet been elucidated. Undoubtedly, osmotic stress and adaptation to salt loading in birds with salt glands lead to concerted alterations of the hypothalamic neuroendocrine activities (HOFFMAN et al., 1977) which may relate directly to the reduced renal fluid volume clearance. However, hormones appear to be of minor importance in the acute adjustments of salt gland function which is mainly under neural control by secretory fibres of Nn. VII and IX. Thus, with respect to the efferent hypothalamic osmoregulatory mechanisms, control of the salt gland and the kidney functions appear to have little in common. This statement does not deny the important roles of hormones as permissive factors in establishing salt gland performance. Concerning afferent hypothalamic osmoregulatory mechanisms, the lack of brain stem osmoreceptors in birds as sensors in the control of salt gland function would fit with the idea of generally less developed receptive functions in the avian as compared to the mammalian hypothalamus which is suggested by the previously mentioned differences in the thermoreceptive capabilities. This would mean that the hypothalamic linkage between renal and salt gland control in birds, as it is indicated by the local temperature dependence of both systems, would be restricted to integrative functions of hypothalamic neurons. The alternative idea that brain stem osmoreceptors act only on the renal osmoregulatory mechanisms (DEUTSCH & SIMON, 1980) would not interfere with this conclusion.

Input factors in salt gland control

The analysis of the afferent mechanisms by which the kidneys and salt glands are controlled in birds has proceeded from the idea that the avian regulation system for fluid and electrolyte balance is analogous to that of mammals. Accordingly, brain stem osmoreceptors have been assumed to control salt gland activity (SCHMIDT-NIELSEN, 1960). In addition, blood volume receptors which are important in mammalian osmo- and volume-regulation have also been taken into consideration as input factors in salt gland control.

Tonicity

Although the idea of brain stem osmoreceptors controlling salt gland activity has not gained experimental support the importance of osmoreception or, more correctly, toni-

TABLE 1: Response of avian salt gland to intravenous administration of various hyperosmotic solutions (from PEAKER & LINZELL, 1975, and own observations). Strong + and weak (+) activation, no change ∅, inhibition —

Solution	Response	Species
NaCl	+	many
Sucrose	+	cormorant, duck, gull, goose
Mannitol	+	duck, gull
Na_2SO_4	+	goose
NH_4Cl	+	duck
LiCl	+	goose
KCl	(+)	duck
Urea	— or ∅	duck
Glucose	—, ∅, (+)	duck

city reception has been convincingly demonstrated by many investigators (PEAKER & LINZELL, 1975). Osmotically active substances with a predominantly extracellular distribution stimulate the salt gland when administered as hyperosmotic solutions (Table 1). The investigations of HANWELL et al. (1972) have presented evidence that at least a significant fraction of the responsible osmoreceptors are located in the central sections of the cardiovascular system.

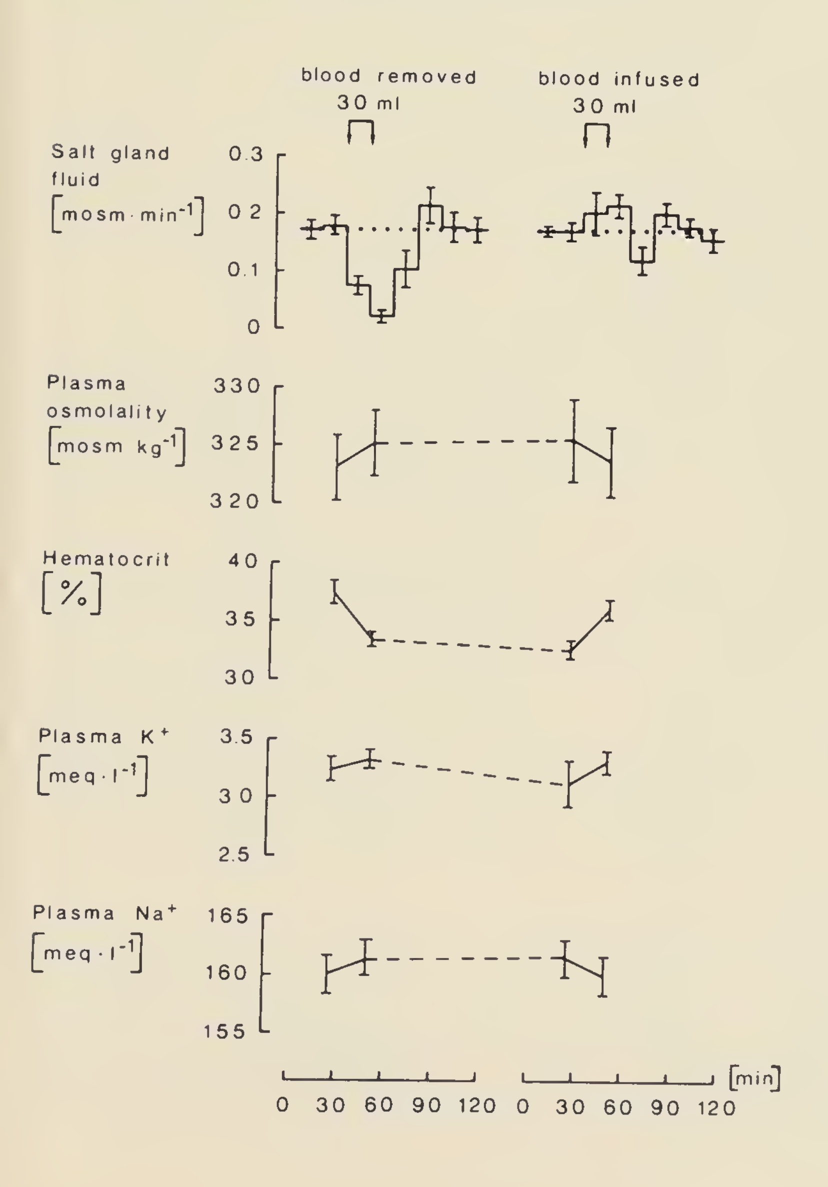


FIGURE 2. Effects of withdrawal and reinfusion of blood on salt gland activity and on plasma osmolality and electrolytes in conscious Peking ducks. The animals received a steady osmotic load of 0.175 mosm · min^{-1} by intravenous infusion of a NaCl solution of 700 mosm · kg^{-1}; means with standard errors of 8 experiments.

Volume

The question whether osmoregulatory signals do exclusively account for salt gland control, and the working hypothesis that blood volume receptors are additionally involved (HOLMES, 1965) have been repeatedly investigated and much debated. In 1975, PEAKER & LINZELL have examined the conflicting reports and arrived at the conclusion that blood volume receptors most likely do not participate in the control of salt gland activity. However, recent publications show that the question of volume factors involved in salt gland control has not been definitely settled (ZUCKER et al., 1977; PEAKER, 1978).

In Peking ducks adapted to chronic salt loading, experimental conditions could be realized in which salt gland activity did not correlate with plasma osmolality nor with plasma Na^+ (HAMMEL et al., 1978; DEUTSCH & SIMON, 1978), indicating that additional input factors must indeed be involved in salt gland control. Therefore, the effects of volume changes on salt gland activity were reexamined. Fig. 2 shows the effects of withdrawing and infusing approximately 15 % of the blood volume on salt gland activity of salt adapted ducks secreting in response to a submaximal load of hyperosmotic NaCl solution. Blood withdrawal caused a temporary inhibition and reinfusion some activation af salt gland secretion. However, this result cannot be considered as unequivocal evidence for salt gland control by blood volume receptors, since the blood volume changes expectedly caused secondary equidirectional changes of the interstitial volume.

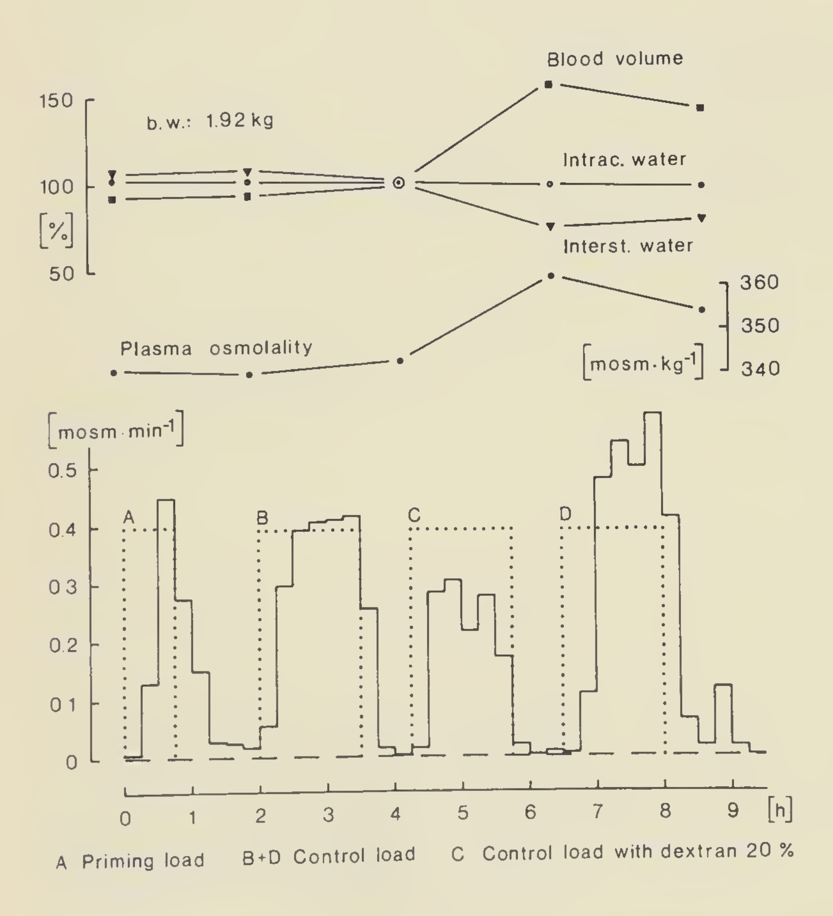


FIGURE 3. Effects of intermittent loading of a conscious Peking duck with NaCl solution of 1000 mosm $\cdot$ kg^{-1} at a rate of 0.4 mosm $\cdot$ min^{-1} with (C) and without (A, B, D) 20 % dextran on salt gland activity and plasma osmolality. The changes in the body fluid compartments were estimated from salt and water in- and output and from changes in hematocrit and red blood cell countings and were based on the measurements of RUCH & HUGHES (1975).

Fig. 3 shows the result of an experimental procedure by which interstitial and blood volumes were changed oppositely under otherwise identical conditions of salt gland stimulation. The first two experimental periods (A, B) of the diagram illustrate a kind of salt loading to which salt-adapted Peking ducks responded predictably so as to

maintain a balanced state between salt input and output. First, NaCl in H_2O solution of a concentration equal to that of the average salt gland fluid, i.e. 1000 mosm · kg^{-1} was infused at a rate of 0.4 ml · min^{-1} until the salt glands were definitely stimulated (A). When the infusion was stopped, the animal gradually reduced its salt gland secretion within some 30 to 45 min until it could be presumed that it had reached the threshold of salt gland activity. This assumption could be verified by the observation that a subsequent standard load consisting in a 90 min infusion of the same solution at the same rate was put out exactly, with a latency of 30 to 45 min, and with a negligible change of plasma osmolality (B). Many control experiments with repeated standard loading have confirmed that input of salt and water by infusion and output by salt gland secretion were balanced within a few percent of the load and at virtually constant plasma osmolalities (HAMMEL et al., 1978). It was presumed that under otherwise identical conditions changes of blood and/or interstitial volume or shifts between these compartments should disturb this balance, if one or the other volume factor was involved in salt gland control (SIMON-OPPERMANN et al., 1978 a). Part C of the figure demonstrates the crucial part of the experiment: The effect of the standard salt load was compared with that of the same load, however, with 20 % dextran added, which is known to be retained in the vascular system according to its high molecular weight (mean of 60,000). Obviously, the response to the standard salt load with the dextran added was definitely reduced. This inhibition was associated with a considerable water shift from the interstitial to the intravascular compartment which could be deduced from the reductions of hematocrit and red blood cell countings and was due to the high oncotic pressure of the dextran. The only partial removal of the salt load caused a rise of plasma osmolality at the end of secretion in period C, i.e. when the animal had returned to the threshold of salt gland activity. This threshold was now characterized by an elevated plasma osmolality and a reduced interstitial volume (or increased blood volume). At this new threshold condition, the animal typically reacted to the final standard load (D) by excreting approximately the same amount of fluid and salt as administered by the load.

The decision whether the reduction of the interstitial volume or the increase of blood volume accounted for the inhibition of salt gland activity follows from a comparison of a variety of experimental procedures affecting salt gland activity and one or both extracellular compartments. Table 2 indicates that the only compartment whose

TABLE 2: Relationship between salt gland activity and changes in the body fluid Compartments to be expected at various experimental conditions (investigations in conscious Peking ducks; + increase, ∅ no change, — decrease)

Experimental condition	Blood volume	Interstitial water	Intracellular water	Salt gland activity
Injection of hyperosmotic NaCl or mannitol solution	+	+	—	+
Blood withdrawal	—	—	∅ –	—
Blood infusion	+	+	∅ +	+
20 % dextran added to osmotic standard load	+	—	∅	—
Infusion of isoosmotic saline	+	+	∅ —	+

changes were directionally correlated with the changes of salt gland activity was the interstitial compartment. Therefore, the statement of PEAKER (1978) "that an increase in blood volume per se does not initiate salt-gland secretion in geese and ducks" is extended by the hypothesis that the interstitial volume is an input factor in salt gland control besides the tonicity of the extracellular fluid.

The way in which a change of interstitial volume influences salt gland activity remains to be elucidated. Receptors somewhere in the body signalling volume changes to the osmoregulatory neurons in the brain have to be taken into consideration. Changes of the interstitial space or pressure in the salt gland itself cannot be excluded as a mode by which salt gland activity is influenced. Whatever the final answer will be, the studies on salt gland control have presented evidence for this quite unexpected possibility of a direct involvement of a fluid compartment in the control of water and electrolyte balance which had previously been assumed to act only indirectly through blood volume changes. The implications of this hypothesis might generally alter our view about the mechanisms of body fluid homeostasis, if its validity could also be demonstrated for other osmoregulatory effector organs in birds and mammals.

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Renal Glomerular and Tubular Contributions to Osmoregulation

William H. Dantzler

Introduction

The kidneys play a central role in osmoregulation in birds by helping to control the excretion of ions and water. Some species of birds also have additional glands for the excretion of ions. Moreover, the composition of the initial urine produced by the avian nephrons may be substantially modified by structures distal to the kidneys before it is finally excreted. Nevertheless, the kidneys are responsible for the formation of the initial urine and are, therefore, quantitatively very important for the regulation of the excretion of ions and water.

In this paper, I shall discuss some of the results that we have obtained by direct studies of individual nephrons and attempt to demonstrate the ways in which regulation of the function of individual nephrons may influence the excretion of ions and water. I shall concentrate primarily on the regulation of glomerular filtration rate, and its relationship to fluid absorption, the osmolarity of the urine, and the excretion of ions and water.

Anatomy of the avian kidney

The avian kidney contains a mixture of nephrons resembling those of reptiles and those of mammals (Braun & Dantzler, 1972). Most nephrons (about 90 % in Gambel's Quail, Braun & Dantzler, 1972; about 70 % in Starlings, Braun, 1978), are of the reptilian-type. They are located superficially in the kidney, consist only of proximal and distal tubules withouth loops of Henle, and drain at right angles into collecting ducts. Thus, they do not function together to contribute directly to the concentrating mechanism of the kidney.

Some nephrons (about 10 % in Gambel's Quail, Braun & Dantzler, 1972; about 30 % in Starlings, Braun, 1978) are of the mammalian type. These are situated deep to the reptilian-type nephrons, have highly convoluted proximal tubules, loops of Henle with thick and thin limbs, and distal convoluted tubules. The loops of Henle from these mammalian-type nephrons, the vasa recta, and the collecting ducts which drain both the reptilian-type and the mammalian-type nephrons are bound by a connective tissue sheath into medullary cones. This arrangement, as in the mammalian kidney, permits the avian kidney to produce a urine hyperosmotic to the plasma.

Changes in overall glomerular filtration rate

Since the rate of formation of ultrafiltrate at each renal glomerulus determines the rate at which fluid is delivered to the lumen of the corresponding proximal tubule, it helps to determine the volume, ionic content, and, possibly, the osmolarity of the final urine. Therefore, changes in the glomerular filtration rate (GFR) may play an important role in osmoregulation.

Department of Physiology, University of Arizona, College of Medicine, Tucson, Arizona 85724, U.S.A.

Clearance measurements of overall GFR (a composite of all the single nephron GFRs) have been made for a number of birds, without salt glands, during different states of hydration or during the intravenous administration of a hyperosmotic sodium chloride solution (1 mol/1) (Table 1). The overall GFR for the gallinaceous birds, at least, tends to decrease with a salt load and increase with a water load. The one passerine species, the Starling, studied in a comparable fashion did not show a decrease in overall GFR with a salt load. However, it should be noted that these birds could not tolerate the same salt load (only 32 mEq/kg body weight) that produced the marked decrease in overall GFR in the gallinaceous birds (about 45 mEq/kg body weight). Some variation in the magnitude of this glomerular response also appears to occur among gallinaceous birds from different habitats. The reasons for these veriations in glomerular response are not yet understood, but the important point for the current discussion is that the overall GFR in some birds, at least, can vary with hydration and, therefore, may contribute to osmoregulation.

TABLE 1: Total kidney glomerular filtration rate (GFR)

Environment and mode of existence	Species	GFR ml kg^{-1} min^{-1} Control	Salt load	Water load
Moist, terrestrial gallinaceous	Chickens *(Gallus gallus)*	1.23 ± 0.04 (137)	0.35 ± 0.04 (20)	3.18 ± 0.04 (77)
Semi arid, terrestrial gallinaceous	Gambel's Quail *(Lophortyx gambelii)*	0.88 ± 0.04 (97)	0.15 ± 0.02 (4)	1.39 ± 0.22 (8)
Moist, terrestrial passerine	Starling *(Sturnus vulgaris)*	2.82 ± 0.08 (34)	2.81 ± 0.21 (5)	—

Values are means ± SE. Numbers in parenthese are sample sizes. Values for chickens are from DANTZLER, 1966, and AMES et al., 1971; for Gambel's Quail, from BRAUN & DANTZLER, 1972, 1975; for Starlings, from BRAUN, 1978.

Changes in single nephron glomerular filtration rates and number of nephrons filtering

Alterations in overall GFR, when they occur, appear to involve primarily changes in the number of glomeruli filtering (DANTZLER, 1966; BRAUN & DANTZLER, 1972, 1974, 1975; BRAUN, 1978). Although variations in the filtration rates of glomeruli that continue to function also occur, variations in the number of glomeruli actually filtering appear to be more important for the regulation of overall GFR and may be of particular importance in the regulation of urine osmolarity.

The concept that changes in overall GFR result from changes in the number of glomeruli filtering was first suggested by our studies on domestic chickens showing that the maximum rates (Tm) for the renal tubular transport of p-aminohippurate (PAH) and glucose varied directly with overall GFR (DANTZLER, 1966). If changes in overall GFR resulted from changes in the amount filtered by each glomerulus with all continuing to function, the Tm for PAH secretion or glucose absorption would not be expected to change since the mass of tissue transporting PAH and glucose would not have changed.

In terms of this type of evidence for changes in the number of filtering nephrons, the avian kidney resembles that of reptiles (DANTZLER & SCHMIDT-NIELSEN, 1966; DANTZLER, 1967) and not that of mammals. However, the avian kidney consists of both reptilian-type and mammalian-type nephrons. We were interested in determining whether a decrease in the number of filtering nephrons during a salt load or dehydration involved both nephron types. We had suggested that only nephrons of the reptilian type, which empty at right angles into collecting ducts and do not function together to contribute directly to the concentrating mechanism, might cease functioning. This would permit nephrons of the mammalian type to continue functioning together, allowing maintenance of the concentrating ability. Since studies of the relationship of the Tm for PAH secretion and glucose absorption to GFR are too indirect to indicate whether apparent changes in the number of filtering nephrons reflect changes in one type of nephron only, we measured single-nephron glomerular filtration rates (SNGFR) directly by the continuous sodium ferrocyanide infusion technique of DE ROUFFIGNAC et al. (1970).

During the salt load which produced the decrease in overall GFR in Gambel's Quail shown in Table 1, virtually all the reptilian-type nephrons ceased filtering (Table 2). Studies in which the renal vasculature was filled with a silicone elastomer indicate that this results from vasoconstriction at the level of the afferent glomerular arterioles (BRAUN, 1976). All the mammalian-type nephrons continued filtering, but there was a small decrease in the SNGFR for these nephrons (Table 2). However, since about 90 % of the nephrons in this avian species are of the reptilian-type, the decrease in the number of filtering reptilian-type nephrons accounted for most of the decrease in the overall GFR observed with the salt load (BRAUN & DANTZLER, 1972). It should also be noted that even during a control diuresis only 71 % of the reptilian-type nephrons were filtering.

During the water load that produced the increase in overall GFR in Gambel's Quail shown in Table 1, all the reptilian-type nephrons were filtering and the SNGFR for both mammalian-type and reptilian-type nephrons approximately doubled (Table 2). Thus, the increase in overall GFR observed in this avian species during a large intravenous water load (about 15 ml of a 125 mosmol/l glucose and saline solution) resulted from a marked increase both in the number of filtering reptilian-type nephrons and in the SNGFR of all nephrons (BRAUN & DANTZLER, 1975).

The separation between the function of the reptilian-type and mammalian-type nephrons is less clear for the one passerine species, the Starling, in which SNGFRs have been measured (Table 2) (BRAUN, 1978). The SNGFRs for the mammalian-type and reptilian-type nephrons during a control mannitol diuresis were virtually the same as those for Gambel's Quail under the same circumstances (Table 2). However, since there are more nephrons in the Starling kidney (about 74,000) than in the Quail kidney (about 47,000), the overall GFR for the Starling was grater than that for the Quail (Table 1). It was not possible to make an accurate determination of the percent of nephrons filtering in the Starling kidney during the control diuresis, but if all the mammalian-type and reptilian-type nephrons were filtering at the observed rates (Table 2), the overall GFR would have been far higher than that actually measured (Table 1). BRAUN (1978) estimated that this overall GFR could be attained if 20 % of the mammalian-type and 45 % of the reptilian-type nephrons were filtering (Table 2). It is not

TABLE 2: Single nephron glomerular filtration rates (SNGFR)

Treatment	Mammalian-type nephrons SNGFR nl min^{-1}	Mammalian-type nephrons percent filtering	Reptilian-type nephrons SNGFR nl min^{-1}	Reptilian-type nephrons percent filtering
	Gambel's Quail *(Lophortyx gambelii)*			
Control (2.5 % Mannitol)	14.6 ± 0.79 (27)	100	6.4 ± 0.20 (41)	71
Salt load (45 mEq/kg)	12.7 ± 0.52 (70)	100	—	0
Water load	33.2 ± 1.57 (155)	100	11.4 ± 0.75 (146)	100
Arginine vasotocin (10 ng kg^{-1})	11.3 ± 0.89 (102)	100	4.7 ± 1.05 (31)	52
(50 ng kg^{-1})	16.5 ± 0.75 (64)	100	6.9 ± 0.42 (26)	26
	Starling *(Sturnus vulgaris)*			
Control (2.5 % Mannitol)	15.6 ± 0.75 (208)	? 20	7.0 ± 0.35 (185)	? 45
Salt load (32 mEq/kg)	14.6 ± 0.61 (28)	? 72	—	0

Values are means ± SE. Numbers in parenthese are sample sizes. Values for control and salt load for quail are from BRAUN & DANTZLER, 1972: for water load, from BRAUN & DANTZLER, 1975; for arginine vasotocin, from BRAUN & DANTZLER, 1974. Values for starlings are from BRAUN, 1978.

at all certain whether the mammalian Type nephrons that are not filtering are small transitional nephrons with short loops of Henle or larger nephrons with long loops. During the maximum intravenous salt load tolerated by the starlings, essentially all the reptilian-type nephrons ceased filtering, but the SNGFR for those mammalian-type nephrons filtering remained at the control level (Table 2). Since the overall GFR did not change, the fraction of mammalian-type nephrons filtering must have increased to about 72 % (Table 2).

Regulation of glomerular filtration rates and number of nephrons filtering by arginine vasotocin

The neurohypophysial hormone arginine vasotocin (AVT) appears to play an important role in regulating the glomerular filtration rate of birds. The intravenous administration of 40 ng AVT/kg caused some depression of overall GFR in chickens (AMES et al. 1971) while as little as 10 ng AVT/kg produced a significant decrease in overall GFR in Gambel's quail (BRAUN & DANTZLER, 1974). Intravenous doses of 50 ng AVT/kg or less had no effect on systemic arterial pressure in either species (AMES et al., 1971; BRAUN & DANTZLER, 1974). These doses appear to be within the range of possible physiological release (MUNSICK, 1964; BRAUN & DANTZLER, 1974).

In Gambel's quail, intravenous doses of 10 ng AVT/kg and 50 ng AVT/kg had no significant effect on the SNGFR of either mammalian-type or reptilian-type nephrons

(Table 2). However, the fraction of reptilian-type nephrons filtering was reduced from 71 % during the control periods to 50 % following 10 ng AVT/kg and 26 % following 50 ng AVT/kg (Table 2). The decrease in overall GFR following these doses was accounted for quantitatively by the decrease in the number of filtering reptilian-type nephrons (BRAUN & DANTZLER, 1974). The results of BRAUN's recent studies (personal communication) on the effects of acute neurohypophysectomy in Gambel's quail also support the concept that AVT helps to control the glomerular filtration rate and the number of filtering nephrons in birds. Following acute neurohypophysectomy, which, presumably, removed endogenous AVT, the mean systemic blood pressure was reduced by about 20 mm Hg, the overall GFR and the SNGFRs for both the mammalian-type and reptilian-type nephrons decreased by 30—40 %, but all the reptilian-type as well as all the mammalian-type nephrons were filtering. These data suggest that AVT exerts a pressor effect to help maintain the normal systemic blood pressure and, therefore, the normal renal blood flow and SNGFR, and that it also regulates the number of filtering reptilian-type nephrons by altering the resistance at the level of the afferent arteriole.

Relationship of the effect of arginine vasotocin on the number of filtering nephrons to the concentrating ability of the avian kidney

Arginine vasotocin appears to be a true antidiuretic hormone in birds (MUNSICK, 1964). Its antidiuretic effect has been considered to result primarily from an ability to increase the permeability of the collecting duct (and, possibly, the distal tubule) to water, thereby permitting fluid in the collecting ducts to equilibrate with the interstitium of the medullary cones (SKADHAUGE, 1964; AMES et al., 1971). However, the effect of AVT on tubular permeability to water has never been documented directly for avian nephrons. Moreover, AVT appears to produce a decrease in overall GFR by reducing the number of filtering nephrons in a manner similar to that observed with a salt load or dehydration. Such a mechanism is practical for the reptilian-type nephrons which do not function together to produce a urine hyperosmotic to the plasma. This mechanism can conserve water at the expense of excreting some ions and nitrogenous waste. More importantly, perhaps, it reduces the volume flow rate through the collecting ducts. In birds, all the reptilian-type nephrons contribute to the fluid flowing through the collecting ducts in the medullary cones. From the data for Gambel's quail in Tabel 2, we can calculate that the volume flow rate through the collecting ducts is reduced by about 40 % from the control level following the administration of 10 or 50 ng AVT/kg. This reduction, resulting primarily from a reduction in the number of filtering reptilian-type nephrons, may be more important than any increase in tubular permeability to water in enhancing the concentrating ability of the avian kidney.

Although the effects of AVT have not yet been evaluated in starlings, a salt load produces a decrease in the number of filtering reptilian-type nephrons similar to that observed in the quail and also an increase in the number of filtering mammalian-type nephrons (Table 2) (BRAUN, 1978, in press). This pattern also may result from the effect of AVT on the distribution of renal blood flow. The decrease in the number of filtering reptilian-type nephrons will reduce volume flow through the collecting ducts and the increase in the number of filtering mammalian-type nephrons will enhance the effec-

tiveness of the countercurrent multiplier system in producing an osmotic gradient from the base to the tip of the medullary cones. Thus, changes in the number of filtering mammalian-type and reptilian-type nephrons both may influence the concentrating ability of the avian kidney.

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Nitrogen Excretion by the Avian Kidney

F. M. Anne McNabb and Roger A. McNabb

Introduction

In birds, the excretion of most waste nitrogen (N) as urate (i.e. uric acid or any other urate compound) may aid in water conservation in both embryonic and post-embryonic life. Historically, there has been abundant recognition of the potential osmotic advantages of excreting urate as a nitrogenous waste in terrestrial vertebrates with cleidoic eggs. In addition, generalizations about the advantages of urate excretion for the adult animal abound in the literature, but these have not been evaluated adequately.

Patterns of excretion of nitrogenous wastes

Total urinary N excretion (O'Dell et al., 1960; Tasaki & Okumura, 1964; Teekell et al., 1968) and plasma uric acid levels (e.g. Okumura & Tasaki, 1969) are positively correlated with dietary N intake of chickens *(Gallus gallus)*. In general, water consumption increases in parallel with protein intake in chickens (e.g. James & Wheeler, 1949), pigeons *Columba livia* (McNabb et al., 1972) and probably in ducks *Anas platyrhynchos* (Stewart et al., 1968). However, when water is limited, chickens on high protein diets reduce their food intake so that protein-N intake equals that on a low protein diet (McNabb et al., 1973 a).

If 50 % of waste N as urate is the criterion, all birds studied to date are uricotelic (see for e.g. Table II, Shoemaker, 1972). Most studies have utilized galliform birds, and despite variation in techniques and experimental conditions, have ranked urate highest (54—87 %), followed by ammonia (3—30 %), then urea (1—12 %). Variations do occur, but there were no consistent statistically significant changes in the proportions of urinary N components in the studies cited above. This generalization also appears to be valid for pigeons (McNabb et al., 1972).

Recently, we have found a statistically significant increase in the proportion of N excreted as urate, when the N: water intake (and thus excretion) ratios were increased in Turkey Vultures *Cathartes aura*. Thus, a carnivorous bird that regularly encounters high N loads, often in the absence of immediately available water, does have the capacity to make an adaptive shift toward the excretion of a higher proportion of relatively insoluble urates (McNabb et al., 1977 a).

The factors that influence production and subsequent excretion of urate, ammonia and urea differ but are not entirely independent, since high protein intake increases the excretion of all three. In chickens, urate excretion parallels protein intake (see studies of N intake cited above) which affects liver urate synthesis (Karawasa et al., 1973 a, b), plasma urate concentrations and the supply of precursors that govern renal urate synthesis (Evans et al., 1971; Quebbeman, 1973; Martindale, 1976). Although plasma urate is filtered at the glomerulus, tubular secretion usually predominates (see review by Sykes, 1972). The urate transport mechanism is located at the peritubular side of the

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, U.S.A.

liver and kidney in urate production changes with protein intake (Evans et al., 1971), so we need to re-evaluate older studies of urate clearance that assumed all urate production in chickens was hepatic. In pigeons, urate production is entirely renal, so urate excretion depends on the delivery of the precursor, hypoxanthine, to the kidney (Edson et al., 1936).

Ammonia excretion by birds appears to be determined by the same factors that are important in mammals: (1) use of ammonia as a buffer for titratable urinary acidity (Wolbach, 1955; Tasaki & Okumura, 1968), (2) the rate of ammonia production and concentration in renal tubular cells (Makarewicz & Zydowo, 1962, and studies of protein intake, cited above) and (3) the rate of urine flow (ducks: Stewart et al., 1968; pigeons: McNabb et al., 1972; chickens: McNabb & McNabb, 1975 a). Ammonia apparently enters the urine by both diffusion and active secretion in exchange for sodium ions.

Urea, present in chicken plasma at low concentrations, is filtered and partially reabsorbed (Pitts & Korr, 1938) with the amount of reabsorption depending on the state of hydration (Skadhauge & Schmidt-Nielsen, 1967). Urea production from dietary arginine occurs in both liver and kidney (Smith & Lewis, 1963; Owen & Robinson, 1964). Urea, accumulated in the medullary cones of the chicken kidney, contributes <0.5 % of the medullary/cortical difference in OP so does not play any appreciable role in urine concentration (Skadhauge & Schmidt-Nielsen, 1967). However, studies of urea handling by the kidney of carnivorous species such as vultures, where urea accounts for 22 % of urine OP, (McNabb et al., 1977 a) might give a different picture.

Efficiency of nitrogen excretion

Generalizations about the renal efficiency of N excretion in birds usually refer only to urate. However, since other compounds can comprise up to 45 % of the urinary N, calculations of water loss should use total N concentrations. Calculations for chickens typically give mean values of 75—160 ml water/g N excreted. The most efficient mammalian kidneys lose only 9—13 ml water/g N excreted (desert rodents, Schmidt-Nielsen, 1964). Chickens studied by Gibbs (1929 b) lost as little as 13.9—17.2 ml water/g N (one hr collections, urate only). We have found similar ratios (16.3 ml water/g N) sustained for 1.5 hrs after feeding turkey vultures a meat diet without additional water (McNabb et al., 1977 a). Thus, even without the additional benefit of cloacal water reabsorption, birds can excrete nitrogen renally almost as efficiently as desert rodents.

Nitrogenous compounds in the osmotic work of the kidney

Urates exist in dissolved, colloidal, and precipitated states in avian urine. Young & Dreyer (1933) demonstrated the existence of colloidal urates in fowl urine. This work led to the idea that colloids were a key factor in the elimination of urate (Sykes, 1971). Urate concentrations (dissolved + colloidal) do exceed theoretical limits and the distribution of renal mucoids in areas of high urate concentration suggests they may be exerting a “protective“ effect on urate colloids (see review, McNabb & McNabb, 1975 b). The maintenance of urate in colloidal form may be important in the proximal

renal cells (Zmuda & Quebbeman, 1975) but the secretion site(s) are unknown and could be important in the dynamics of urate handling. The relative importance of the parts of the nephrons, but urate precipitation must begin in the distal parts since abundant precipitates often are visible in small, cortical collecting ducts. More than 90 % of the urate is precipitated in ureteral urine at urate concentrations of 1800 mg% and higher in both chickens (McNabb, 1974) and pigeons (McNabb & Poulson, 1970). Both these species can produce 10 × this urinary urate concentration, so colloids comprise a trivial proportion of the final urinary urate concentration in most urine samples.

Few attempts have been made to compare uricotelism in birds to ureotelism in mammals with respect to the OP's that must be generated by the kidney. Sykes (1971), using data on chickens with high water turnover, calculated only 18 mOsm/l OP would be contributed to the urine if all urate N excreted was present instead as urea. He felt this small osmotic load could be accommodated easily by the fowl's kidney (typical urine OP's are 100—500 mOsm) and, that the biological significance of uric acid excretion lies only in its value to the cleidoic egg. We feel that only data reflecting the ability of the kidney to produce high urinary uric acid concentrations should be used to evaluate the osmotic advantages of urate excretion, when water is limited. We used data on chickens to calculate the OP of solutions with comparable amounts of N as urea. The highest values from many studies would either exceed or utilize essentially all of the osmotic potential of the chicken kidney. For e.g. we calculate potential OP's as urea up to 478 mOsm for 24 hr collection periods (O'Dell et al., 1960), up to 936 mOsm for 8 hr collections and up to 2571 mOsm for one hr collections (Gibbs, 1929 b). Turkey vultures, in the period after feeding, would have to produce a urine of > 2189 mOsm to excrete all N as urea; the actual urinary OP was 417 mOsm (McNabb et al., 1977 a). These calculated values for vultures would exceed the concentrating ability of even salt marsh Savannah Sparrows *Passerculus sandwichensis beldingii,* which have the most efficient avian kidneys known (Poulson & Bartholomew, 1962 a).

A second important factor for minimizing renal osmotic work is the coprecipitation of cations with urate. This subject has received little attention and failure to appreciate the possibility of coprecipitation has resulted in most studies of avian electrolyte excretion measuring only the cations in the liquid fraction of the urine and generally underestimating the ability of the avian kidney to excrete cations. When both the liquid and precipitated fractions of chicken urine are analyzed, up to 75 % of the Na^+ and 34 % of the K^+ are coprecipitated with urate (McNabb et al., 1973 a). Concentrations of $Na^+ + K^+$ would have been up to 87 mEq/l higher if these cations from the precipitate had been equally distributed throughout the urine samples; a fairly significant effect in the context of chicken kidneys that usually do not produce urinary OP > 500 mOsm. In addition to monovalent cations, up to 32 % of the Ca^{++} and 24 % of the Mg^{++} may be included in the precipitate (McNabb & McNabb, 1977 b).

Urinary precipitates appear to consist of layers of uric acid dihydrate interspersed with layers of soluble cations "bound" by charge configurations. Evidence for this picture comes from X-ray diffraction studies (Lonsdale & Sutor, 1971), molar ratios of cations: urate > 1.0, thermogravimetric analysis and differential thermal analysis (McNabb & McNabb, 1973 a, 1974, 1975 b, 1977 b). We have no information on the mechanisms leading to coprecipitation of cations with urate.

Adaptations for the elimination of precipitated urate

The unique morphology of the avian kidney, in which medullary regions are arranged in a tree-like system of medullary cones branching from the ureter, may play a role in urate elimination. In photographs of medullary injection casts of the kidneys the collecting ducts in medullary cones appear longer and straighter in primarily carnivorous species than in granivorous species (Johnson et al., 1972). This observation is consistent with the idea that the type of medullary branching, without regions where pooling would occur, is important in the elimination of large amounts of precipitated urate from the avian kidney (Poulson, 1965).

Mucoidal macromolecules are abundant in the collecting ducts and all levels of ureteral branches of canary, chicken and pigeon kidneys (Longley et al., 1963; McNabb et al., 1973 b). Thus, mucoid abundance where precipitated urates are present, suggests they function as lubricants and/or in "binding" together masses of precipitated urates.

In the urine of birds and reptiles, urates precipitate in the form of tiny spheres rather than as crystals seen in mammalian urine. Minnich & Piehl (1972) suggested these spheres act as miniature ball-bearings and facilitate flow of the urinary suspension. In scanning electron micrographs of freeze dried Japanese quail kidneys, spheres (0.5—8.5 μm diameter) are present in ureteral branches and medullary collecting ducts, and appear occasionally in cortical collecting ducts (McNabb & McNabb, unpublished). Further improvements in tissue preservation should allow use of scanning electron microscopy for determination of the "earliest" site within nephrons where sphere formation occurs.

Recently, we have produced urate spheres in vitro, similar to those found in avian urine, when abundant Na^+ions are present in a solution containing excess uric acid. The addition of proteins (to test mucoid influences) to these in vitro systems facilitates supersaturation of the liquid phase (presumably due to colloid formation) but prevents sphere formation and results in the exclusion of Na^+ by K^+ from the precipitate. Thus, urate sphere formation with cation incorporation may be primarily due to the intrinsic properties of urates rather than biological events (McNabb & McNabb, unpublished).

In removal of urine from the kidneys, peristaltic movements may help "milk" urine, containing precipitated urate, from ureteral branches in medullary cones into, and down, the ureters (Gibbs, 1929 a). Finally, although we have emphasized the kidney adaptations to high urate excretion, further water reabsorption in the cloaca or intestine must be the final step in those species that eliminate urinary components as a semisolid paste attached to fecal material.

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Quantitative Interaction of Kidney and Cloaca in Bird Osmoregulation

Erik Skadhauge

Introduction

It is well known that the droppings of birds consist of a mixture of uric acid, urates, and faeces. This is due to storage of ureteral urine together with faeces in the cloaca. The storage takes place in the lowest parts of the intestine denoted corpodeum and colon. These parts have a resorptive epithelium (Johnson & Skadhauge, 1975). The excretion of salt and water — and conservation during water or salt lack — is therefore not solely determined by the kidney. The cloacal sojourn may either assist or counteract the function of the kidney. The interaction of kidney and cloaca in determining final salt and water output in various osmotic situations is thus a major problem in bird osmoregulation (Skadhauge, 1973). As reptiles, the other uricotelic group of vertebrates, birds are preadapted to water-lack as the majority of nitrogen is excreted as insoluble uric acid and urates requiring little water. In contrast to what happens in reptiles the cloacal sojourn poses problems, since birds, as mammals, have a diluting-concentrating kidney. What happens in the cloaca to the dilute urine formed in the hydrated state, and what happens to the concentrated urine formed in the dehydrated state? And is the excretion of NaCl and other ions changed during the sojourn in the cloaca?

This survey will summarize our present knowledge from a quantitative view-point. In the first section the composition and flow rate of urine will be presented. In the second the cloacal transport parameters will be discussed. In the third section the interaction of kidney and cloaca will be quantitatively assessed.

The majority of physiological studies have been carried out on the domestic fowl, but comparisons with other birds have shown that it is a good denominator for granivorous, terrestrial birds. The special problems for birds with salt-glands will be mentioned, and the excretory problems of birds which have a high salt intake, but no salt gland, will be discussed.

Flow-rate and composition of urine

Collection of "pure" ureteral urine requires some operation or cannulation. If, however, the natural droppings are collected under oil in a cooled tray, the liquid part of the droppings or that rich in uric acid reflects fairly precisely the composition of ureteral urine (Skadhauge, 1974 a). This permits determination of concentrations, but not of flow rates. Even during adequate collection of ureteral urine disturbance diuresis is a problem in dehydrated or normally hydrated birds and disturbance antidiuresis a problem in hydrated birds. General anaesthesia usually leads to some loss of concentrating ability. Permanent separation of ureters and cloaca leads to infection, salt-depletion, polydipsia, and inevitably poor growth rate (Skadhauge, 1973). For these reasons concentrating ability has been measured for several birds, but correlation of flow-rate and

Department of Medical Physiology A, The Panum Institute, University of Copenhagen, Blegdamsvej 3 C, DK-2200 Copenhagen N, Denmark.

TABLE 1: Osmolality and electrolyte concentrations of ureteral urine in dehydrated birds. (from SKADHAUGE, 1977, and SKADHAUGE, 1974 a)

	Osmolality mOsm	Electrolyte concentrations Na$^+$	Cl$^-$ mequiv/l	K$^+$
Chicken *Gallus gallus*	582	41	36	73
Galah *Cacatua roseicapilla*	982	24	19	125
Red Wattle bird *Anthochaera carunculata*	917	25	71	201
Zebra Finch *Taeniopygia castanotis*	1005	8	40	135
Emu *Dromaius novaehollandiae*	459	6	5	120
Kookaburra *Dacelo gigas*	944	28	10	93

composition of ureteral urine (osmolality and ionic concentrations) is only available for a few species. Table 1 lists maximal urine osmolality and concentrations of "strong" electrolytes from selected species. In Table 2 flow-rate and urine osmolality are presented for the hydrated and dehydrated domestic fowl, together with osmolality of the cloacal contents.

Inspection of Table 1 permits three conclusions: First, renal concentrating ability is limited in birds, generally with maximal osmotic urine to plasma ratios of 2—3. Only in a few salt marsh sparrows have higher values been found. Second, NaCl constitute a small fraction of total osmolality in seed-eaters. Third, there is little correlation between renal concentrating ability and degree of xerophilia (SKADHAUGE, 1974 a). This finding is in contrast to the condition in mammals; it testifies to the importance of the interaction of kidney and cloaca to modify total excretion.

Table 2 shows first the great variability in the flow-rate and concentration of ureteral urine. Second, the composition of the contents of coprodeum and colon are greatly influenced by that of ureteral urine. The change in flow-rate from hydration to dehydration is largely due to an increased renal resorption of water. The rate of solute

TABLE 2: Flow rate and osmolality of ureteral urine, and osmolality of cloacal contents in the domestic fowl. (from SKADHAUGE, 1973)

	Flow rate ml/kg · hr	Osmolality Urine	Coprodeum mOsm	Colon
Dehydration	1.08	538	489	376
Hydration	17.9	115	143	192

excretion is only moderately reduced in response to dehydration, largely due to a falling glomerular filtration rate.

The low concentration of NaCl in solution has prompted studies of the contribution of other ions to total urine osmolality. In the domestic fowl as well as in a xerophilic Australian parrot, the Galah, and in a large flightless bird, the Emu, does potassium-ammonium-phosphate constitute the majority of the osmolality. In dehydrated domestic fowl receiving a wheat and barley diet the average concentrations were NH_4^+:120, PO_4^{--}:130, and K^+:73 mequiv/l (SKADHAUGE, 1977 a).

Cloacal transport parameters

The presence in the gut of anisotonic fluids of varying ionic composition necessitates the study of dependence of water and ion transfer upon osmolality and concentration of ions, first Na^+ and Cl^-, but also K^+, NH_4^+ and PO_4^{---}. Two types of experiments have been used: Intraluminal in vivo perfusions, and in vitro mounting of the epithelium in the Ussing-chamber. The former elucidates water movements and net transport rates and dependence upon osmotic condition and NaCl balance of the animal. The latter is most suitable for determination of the ionic movements, particularly unidirectional isotope fluxes. The findings have been summarized for the domestic fowl (SKADHAUGE, 1973) and for other granivorous birds (SKADHAUGE, 1978 a). In the domestic fowl a fairly large number of relevant transport parameters have been measured. This includes osmotic water permeability coefficient in the two directions, magnitude of solute-linked water flow, i.e. water absorbed in the absence of an osmotic difference from lumen to plasma, generally driven by Na(Cl) transport; the K_t (concentration at half maximal flow rate) and J_{max} (maximal flow rate) values for sodium transport which is correlated to the luminal sodium concentration by saturation kinetics, and net transport rates for K^+, Cl^-, NH_4^+, and PO_4^{---}. The absorption of Cl^- and NH_4^+, and secretion of K^+ is largely determined by the net sodium absorption rate (SKADHAUGE, 1978 b). The most important transport parameters are stated in Table 3 for fowl and Galah. Most perfusions have been carried out with fluids of plasma-like ionic composition, or solutions resembling the composition of ureteral urine in the dehydrated state. The reason for this is that dehydration presents the biggest problem for resorption of ureteral urine in the cloaca.

The main result of the in vitro experiments is that in bird coprodeum and colon, as in several other epithelia, the primarily transported substance is the sodium ion (CHOSHNIAK et al., 1977; SKADHAUGE, 1978 b, c). Furthermore, it is an electrogenic transport

TABLE 3: Cloacal transport rates for salt and water in the domestic fowl and the Galah. (from SKADHAUGE, 1973, and SKADHAUGE, 1974 b)

	Transport rates Na^+	Cl^-	K^+	Osmotic permeability	Solute-linked water flow
		µequiv/kg · hr		µl H_2O/kg · hr · mOsm	µ 2 H_2O/µequiv Na^+
Fowl	+175	+42	−97	3.2	+1.1
Galah	+ 88	+82	− 6	0.85	+5.0

Isosmotic perfusion solutions of NaCl with 40 mequiv/l K^+ were used. Absorption is denoted +, secretion −.

with sodium transport primarily being responsible for the generation of a lumen negative electric potential difference (PD). When in the in vitro Ussing-chamber identical bathing solutions are present on the two sides, and the PD nullified by a so-called external short-circuit current no driving force exists for ion movements across the tissue. In this situation the flux-ratio for chloride is unity demonstrating the passing nature of the transfer of this ion. The fairly large transport seen in vivo (Table 3) can be accounted for by the electrical driving force (the PD). Measurement of the unilateral sodium fluxes show that sodium transport accounts largely for the short-circuit current as observed in several other epithelia.

Some observations have been carried out on other birds, particularly the Galah. The main finding is that weight for weight (as the same functional segment has been perfused) a very close agreement between the ion transport parameters in the fowl and in Galah have been found both in vivo and in vitro. Some rather subtle differences in transport patterns do, however, fit with the teleological assumption of the Galah being better adapted to life with lack of salt and water. From Table 4 it will appear that the

Table 4: Transport parameters measured for coprodeum in vitro in the domestic fowl and the Galah.
(from Choshniak et al., 1977, and Skadhauge, 1978 b)

	Electric potential difference	Resistance	Unidirectional ion flux, serosa-mucosa	
			Na^+	Cl^-
	mV	Ohm · cm^2	μequiv/cm^2 · hr	
Fowl	37	132	1.4	2.2
Galah	19	91	2.3	3.7

Galah has a more permeable epithelium: Lower resistance, higher unidirectional fluxes of Na^+ and Cl^- in the serosa to mucosa direction. This is associated—as to be expected from studies of other epithelia—with a low sodium concentration of solute-linked water flow (Table 3). This means that more water will be absorbed per sodium ion. Since in the Galah the osmotic permeability coefficient is lower (Table 3) better conditions exist in this species for water absorption from the hyperosmotic ureteral urine (Table 1).

Finally, since the Galah coprodeum gets a more concentrated urine with a higher K^+ concentration it is relevant that high K^+ in this bird does not suppress net Na^+ absorption as much as in the fowl.

Reaction to osmotic stress has been elucidated both in the fowl and in the Galah. The sensitivity of the cloacal transport parameters to hydration/dehydration was not marked (Skadhauge, 1973). In the fowl hydration induced a smaller osmotic permeability coefficient, but only in the mucosa to serosa direction, and a fall in apparent K_t for sodium transport. Salt loading/depletion did in contrast to this induce most significant changes in sodium transport (Table 5). In both fowl and Galah did a high NaCl-diet decrease the sodium transport of the coprodeum as compared to a low sodium diet. The difference was pronounced in vivo (Thomas, Skadhauge & Read, 1975), in vitro, however, the effect was dramatic. Net sodium transport and short-circuit current

TABLE 5: Net sodium transport (short-circuit current) across coprodeum and colon in the domestic fowl and the Galah.
(from: CHOSHNIAK et al., 1977, and SKADHAUGE, 1978 b)

	Coprodeum		Colon	
Diet:	Low salt	High salt	Low salt	High salt
Fowl	284	7	275	227
Galah	210	2	81	123

(unit: μAmp/cm^2)

were almost suppressed to zero. In contrast to this little change was seen in the colon (Table 5). In the Galah the sodium transport of colon was even augmented during sodium loading. The findings both of fowl and of Galah must, however, be interpreted with some caution. In contrast to coprodeum the colon during sodium-loading, but not during sodium-depletion, requires presence of amino acids. The findings in the Galah may be due to less viability of the preparation in the sodium-depleted birds. Taken together these findings do agree with the 50 % reduction in sodium transport observed in vivo for both segments perfused together. It is outside the scope of this presentation to discuss the mechanisms of these changes. Suffice to say that aldosterone is partly responsible as it restores one quarter of the sodium transport in coprodeum and three quarters in colon. The different sodium sensitivity of colon and coprodeum makes it reasonable to suggest that colon always resorbs an important fraction of salt and water from chymus, whereas coprodeum regulates very precisely the final NaCl absorption from both faeces and urine (SKADHAUGE, 1978 b).

Interaction of kidney and cloaca

When knowledge of renal excretory rates and cloacal resorptive capacity is at hand, the interaction of kidney and cloaca in osmoregulation can be quantitatively assessed. A rational way of comparing the salt and water relations of the two organs is to estimate the maximal quantitative modification cloacal sojourn can impose upon water and ion excretion from the kidney (SKADHAUGE, 1977 b). A summary of these findings is given in Table 6 for the domestic fowl. It will be seen that the large flow-rate of urine in the water and salt-loaded states respectively makes water resorption and salt conservation in the cloaca insignificant when the organism wants to rid itself of these substances. During dehydration, however, an important amount of Na(Cl) is resorbed. Water is not lost, as to be expected from the osmolality of ureteral urine, but on the

TABLE 6: Fractional absorption of water and electrolytes in the cloaca from ureteral urine in the domestic fowl.
(from SKADHAUGE, 1977 b, and SKADHAUGE, 1978 a)

Dehydration	H_2O	+14 %	Normal hydration low salt diet	Na^+	+90 %
	Na^+	+69 %		Cl^-	+80 %
Hydration	H_2O	+ 2 %		K^+	−20 %
Salt loading	Na^+	+ 2 %		NH_4^+	+10 %

Absorption is denoted +, secretion −.

contrary, a small amount is saved. There is a significant cloacal K^+ secretion, whereas only 9 % of NH_4^+ is resorbed, and PO_4^{---} comes close to undergoing no net absorption (SKADHAUGE, 1978 c). Since a combined lack of salt and water is common for seed-eating birds this kidney-cloaca interaction is teleologically reasonable. Furthermore, were the renal NaCl conservation more complete, uric acid and urates might perhaps clogg the ureteral tree as salts help these substances stay in colloid suspension.

Xerophilic seed-eaters such as the Budgerygah (SKADHAUGE, 1973) and the Galah (SKADHAUGE, 1974 b) seem largely to behave as the domestic fowl. This pattern of kidney-cloaca interaction with its precisely matched balance between the two organs may be the most widespread among birds. Although studied in much less detail two other patterns may exist: In the first of these the kidney plays a smaller role in water conservation, the cloaca a larger, and in the second excretion of salt and water is primarily determined by the kidney with the cloaca acting like a mammalian bladder. Finally, a third pattern may exist in birds with salt-glands. These problems will be considered in the last section.

Special problems

An unexpected low renal concentrating ability in the Emu (Table 1) led to the idea that this bird as a member of the ratite group might have a more "reptilian" (SKADHAUGE, 1978 d) kidney-cloaca interaction than other birds. Cloacal studies, in progress, seem to confirm this concept: NaCl absorption capacity is large, and the sodium concentration of the solute-linked water flow is close to isotonicity. The cloaca is thus geared to absorb the urine which is produced by the kidney and to lose little water. The second pattern is that of birds which may drink saline solutions and have no salt gland such as the Zebra Finch (SKADHAUGE & BRADSHAW, 1974). Since the sodium absorption of the coprodeum is presumed to be suppressed and the renal concentration ability is high, these birds may use the coprodeum just as a bladder. The cloaca of these birds should be studied.

Finally, the problem comes of birds with salt glands: When marine birds cope with a high salinity diet of invertebrates they secrete through the salt gland, as determined in the duck, 90 % of the salt in a solution of approximately 1200 mOs (HOLMES, 1975). This is about the double of the renal concentrating ability of most birds. It is possible that the kidney/cloaca system may interact with the salt gland to save water: If salt is cycled from kidney to cloaca and absorbed here with water, and salt excreted through salt gland, "free water" is saved. Some marine birds augment the upper intestinal absorption when exposed to a high oral salt load. An augmentation of the cloacal sodium absorption during salt loading would help the aforementioned hypothesis. Preliminary investigations in the duck, both the domestic duck and the wild Mallard indicate, however, that the sodium absorption of the coprodeum, as judged by the short-circuit current, is just as decreased by salt-loading as found in the fowl (Table 5). A high sodium transport of the colon will, however, save the hypothesis .

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For all literature before 1973 the reader is referred to the author's monograph (SKADHAUGE, 1973).

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Hormonal Control of Water and Electrolyte Transport by the Avian Intestine

David H. Thomas

In order to demonstrate physiological control of intestinal transport, it is necessary to show that function alters appropriately in response to maintenance conditions or metabolic requirements, and that adaptive responses can be reproduced by specific controlling agents. Several studies show that the avian intestine is susceptible to environmental, humoral and pathological influences. Most studies have used domestic fowls *(Gallus gallus)*; results reported here refer to this species unless another is mentioned.

Sodium transport

Actual in vivo intestinal transport rates in the presence of normal intestinal fill can be measured using an inert marker technique. Calculations from data of Hurwitz et al. (1970) give this information for Na^+ transport. There is a very large (pre-)duodenal Na^+ secretion (= net serosal-mucosal flux) which is almost entirely absorbed again in the rest of the small intestine. This Na^+ secretion-reabsorption is approximately equivalent to the turnover of the birds' total body Na^+ pool once per day. Despite the rapid Na^+ turnover anteriorly, it is regulation of the comparatively low Na^+ absorption rates in the fowl coprodeum and colon (CC segment) which determines overall Na^+ balance. Sodium absorption in the CC segment is a primary active process, the rate of which depends both on the luminal Na^+ concentration and on the epithelial transporting capacity (Bindslev & Skadhauge, 1971 b; Thomas & Skadhauge, 1978 a; Thomas et al., 1975). In the CC segment active Na^+ absorption largely determines the rates of associated Na^+-linked transport processes (K^+ secretion, and NH_4^+, Cl^- and non-osmotic water absorption: Thomas & Skadhauge, 1978 a, b).

Na^+-depletion and aldosterone effects

The fowl CC segment responds adaptively to dietary Na^+ restriction (Choshniak et al., 1977; Thomas & Skadhauge, 1978 a; Thomas et al., 1975). In birds maintained on commercial poultry food (117 m mol Na^+/kg food) potential Na^+ absorption rates (as determined by in vivo luminal perfusion or in vitro techniques) were low, and relations between absorption rates and luminal concentrations suggested a diffusive rate-limiting step. Maintenance on a low Na^+ diet (wheat and barley: 2.6 m mol Na^+/kg food) resulted in substantially increased Na^+ reabsorptive capacity and establishment of a saturable (probably carrier-mediated) rate-limiting transport step. This increased Na^+ absorptive capacity would be somewhat offset by diminished Na^+ concentrations in the CC segment lumen (because of diminished ureteral urine concentrations from about 141 to 41 m mol Na^+/l: Skadhauge, 1977), but it is likely that the balance of these two effects would still result in increased actual in vivo absorption of Na^+ by the CC segment from about 29 to 38 μ mol Na^+/kg body weight. (Thomas & Skadhauge, 1978 a).

Department of Zoology, University College, University of Wales, Cardiff CF1 1XL, Great Britain

Aldosterone may be the natural mediator of these responses to low Na^+ diets, because a wheat and barley diet significantly enhanced circulating aldosterone concentrations (9.55 ± 0.64 (SEM) pg/100 μl plasma, compared to 5.78 ± 1.34 pg/100 μl in birds on a commercial diet; n = 4 for each sample, t (6) = 2.54 for the difference, and P < 0.05: ASSENMACHER, SKADHAUGE & THOMAS, in preparation), and because aldosterone injections mimicked some of the Na^+-depletion effects in birds maintained on commercial poultry food. Sodium absorption rates increased 4-5-fold by 5 h after acute intravenous aldosterone injections (120 μg/kg body weight; THOMAS et al., 1975, 1978). Chronic aldosterone injections (2 d × 60 μg/kg · day) had a similar effect, and also established the saturable rate-limiting step for Na^+ transport which is characteristic of Na^+-depleted birds (THOMAS & SKADHAUGE, 1978 c).

Na^+ loading and corticosterone effects

Sodium loading (15.4 m mol NaCl/kg body weight.day orally) of fowls consuming 3.4 m mol Na^+/kg.day in a normal commercial food did not engender any marked change in coprodeal-colonic function in vivo (THOMAS & SKADHAUGE, 1978 a) or in coprodeal function in vitro (CHOSHNIAK et al., 1977). A much larger load (45 m mol NaCl/kg.day orally, plus 10 m mol/kg intravenously before experiment) reduced CC segment NaCl absorption by 50—100 %, and K^+ secretion by more than 50 % (SKADHAUGE, 1967). Control of this effect is uninvestigated.

Domestic ducklings responded to maintenance on 60 % seawater by (among other things) a 60—80 % increase in jejunal and ileal Na^+-linked water absorptive capacity (measured as mucosal transfer from isosmotic media by everted sacs; CROCKER & HOLMES, 1971). In vivo, this response presumably results in a net gain of free water when allied to salt gland NaCl excretion, just as it does in marine teleosts. Corticosterone seems to mediate the response, because 0.5 mg (injected intramuscularly in vivo) mimicked the effects of 60 % seawater, while metyrapone (which blocks corticosterone and aldosterone synthesis) also blocked the response to hyperosmotic maintenance conditions (CROCKER & HOLMES, 1976). Spironolactone also prevented the intestinal response to 60 % seawater, which was interpreted as indicating aldosterone mediation (CROCKER & HOLMES, 1971), but spironolactone can also block the intestinal effects of corticosterone (CROCKER & HOLMES, 1976), In ducks, therefore, corticosterone can be seen to produce a coordinated response to a hyperosmotic environment, enhancing and maintaining both solute-linked water absorption by the intestine and NaCl excretion by the salt glands (THOMAS & PHILLIPS, 1975).

Small amounts of crude oil (such as seabirds are liable to ingest) inhibit solute-linked intestinal water absorption in ducks (CROCKER et al., 1975) and intestinal transport and food intake in gulls and auks (PEAKALL et al., 1978). Thus, oil-polluted seabirds may suffer from severe (perhaps fatal) osmoregulatory distress, and it may be of practical value in rehabilitation of oiled birds that corticosterone will counteract the effects of oil on intestinal transport (CROCKER & HOLMES, 1976).

Calcium transport and its control

Small intestinal calcium absorption represents a variable fraction (< 1) of Ca^{2+} ingestion, with the duodenum and upper jejunum accounting for absorption of

87—124 % of net small intestinal absorption (Hurwitz et al., 1973). Absorption in the duodenum and jejunum is probably largely passive, and luminal Ca^{2+} activity (dependent on Ca^{2+} ingestion and dissolution in the crop, proventriculus and gizzard: Mongin, 1976 a, b) is the main determinant of the Ca^{2+} electrochemical gradient (Hurwitz & Bar, 1969). The passive permeability of the small intestine to Ca^{2+} (calculated from Hurwitz & Bar's 1969 data) is greatest in the duodenum and diminishes posteriorly to a low value in the ileum. In laying fowls, Hurwitz et al. (1973) showed an increased upper jejunal Ca^{2+} permeability (favouring increased Ca^{2+} absorption) during eggshell formation, but P. Mongin (pers. comm.) could find no such change. Ileal Ca^{2+} transfer in either direction may be against the prevailing electrochemical gradient, involving secretion in high Ca^{2+}-diet birds and absorption in Ca^{2+}-depleted birds (Hurwitz & Bar, 1969). Thus ileal Ca^{2+} transfer appears essentially homeostatic (and it may be a site for fine control of Ca^{2+} balance), in contrast to transfer by the anterior small intestine, where absorption (only) occurs at rates directly proportional to dietary Ca^{2+} availability.

Intestinal Ca^{2+} absorption is enhanced by dietary Ca^{2+}-depletion and during the laying cycle at the shell formation stage, but the two responses may be differently mediated and will therefore be discussed separately. Responses to dietary Ca^{2+}-depletion are apparently mediated similarly in mammals and galliform birds. The main hormonal antagonist is 1,25-dihydroxy-cholecalciferol (1,25-DHCC). In mammals, 1,25-DHCC is synthesised from an inactive precursor (cholecalciferol, vitamin D_2) by hepatic 25-hydroxylation and then renal 1-hydroxylation, and it acts directly on intestinal epithelial cells to increase Ca^{2+} transporting capacity (Avioli, 1972). There is sufficient evidence for critical steps in this chain of events to suggest that a similar system operates in birds. Edelstein et al. (1975) demonstrated diet-sensitive double hydroxylation of vitamin D. Chicks injected with radioactively labelled cholecalciferol had labelled 1,25-DHCC appear in intestinal mucosal cell nuclei, and cellular concentrations of 1,25-DHCC and Ca^{2+}-specific binding protein (CaBP) increased in response to dietary Ca^{2+} (or phosphorus) depletion. In agreement with this, chicks responded to dietary Ca^{2+}-depletion by hypocalcaemia, by increased activity of renal 25-HCC-l-hydroxylase and by increased duodenal Ca^{2+} uptake capacity (Friedlander et al., 1977; Swaminathan et al., 1977). In birds, parathyroid hormone (PTH) and calcitonin (CT) counteract hypo- and hypercalcaemia respectively (Assenmacher, 1973), but apparently do not have direct effects on Ca^{2+} uptake and transfer by chick embryo duodenal preparations (Corradino, 1976). (In mammals, PTH and CT probably affect intestinal Ca^{2+} uptake only indirectly, via effects on renal vitamin D hydroxylation pathways: Habener & Niall, 1974.)

Despite the general correlation between intestinal CaBP concentrations and Ca^{2+} transporting capacity (Swaminathan et al., 1977), CaBP is evidently not directly concerned with Ca^{2+} translocation, because Ca^{2+} transport rates increased and peaked some hours in advance of increasing and maximum cellular CaBP concentrations in rhachitic chicks injected with 1,25-DHCC (Spencer et al., 1976; Morrissey et al., 1978).

Actual in vivo Ca^{2+} absorption rates in Quails *(C. coturnix japonica)* and fowls increase during eggshell formation. This response may be independent of 1,25-DHCC stimulation, because it was not associated with changes in renal 25-HCC-1-hydroxy-

lase activity or intestinal CaBP concentrations, and occurred in addition to stimulation by 1-α-HCC (Bar et al., 1976; Montecuccoli et al., 1977). Increased intestinal Ca^{2+} absorption at eggshell formation may be due to a combination of increased Ca^{2+} permeability (see above) and augmented driving forces for passive transfer, because voluntary Ca^{2+} intake (Mongin & Sauveur, 1974) and gastrin secretion (P. Mongin, pers. comm.) both increase and presumably contribute to the raised Ca^{2+} concentrations observed in the small intestine at this time (Mongin, 1976 a). In addition, oestrogens mobilise bone Ca^{2+} during eggshell formation (Assenmacher, 1973) and might conceivably promote intestinal Ca^{2+} uptake at the same time, but this seems not to have been investigated.

Dehydration effects on water transport

In the fowl small intestine, Mongin (1976 a) measured mean maximum luminal osmolalities of 625—750 m osmolal (upper jejunum) and a steady decrease posteriorly to 410—490 m osmolal (lower ileum). Even allowing for the leakiness of the small intestine (reflexion coefficient (σ) 0.49 in the dodenum, 0.75 in the lower jejunum: Mongin & de Laage, 1977; P. Mongin, pers. comm.) driving forces nonetheless favour serosal-mucosal osmotic flow. In the coprodeum and colon (σ = 1.0: Bindslev & Skadhauge, 1971 a; Thomas & Shadhauge, 1978 b) luminal fluid is hypertonic during dehydration and hypotonic in hydrated birds (Skadhauge, 1968). In addition to osmotic flow, there is evidence of Na^+-linked water absorption in the small intestine of fowls (Mongin, 1976 a), ducks (Crocker & Holmes, 1971) and three North American quails *(Lophortyx californicus, L. gambelii* and *Colinus virginianus*: McNabb, 1969) and in the large intestine of fowls (Bindslev & Skadhauge, 1971 b; Thomas & Skadhauge, 1978 b) and the Galah *(Cacatua roseicapilla*: Skadhauge, 1974).

Dehydration of fowls (mean weight loss 7 %) changed in vivo coprodeal-colonic function: the luminal concentration for half-maximal Na^+ absorption rate was reduced, while Na^+-linked water absorption became more effective (1.5 compared to 1.1 μl water per μ mol Na^+: Bindslev & Skadhauge, 1971 b). Both effects would tend to improve water conservation, but it is doubtful whether the increased permeability for mucosal-serosal osmotic flow (also observed in response to dehydration: Bindslev & Skadhauge, 1971 a) would have any effect on water conservation since the normal osmotic gradient in dehydrated fowls favours serosal to mucosal osmosis (Skadhauge, 1968). Since the birds in Bindslev & Skadhauge's (1971 a, b) study were effectively Na^+-depleted (starved for 24 h before experiment) as well as dehydrated, it is possible that the effects on Na^+ transport resulted from endogenous aldosterone secretion. However, dehydration is known to inhibit food consumption in birds (e.g. in *Streptopelia risoria:* McFarland & Wright, 1969), so aldosterone release may be effectively part of the normal response to dehydration anyway.

Arginine vasotocin (the natural avian antidiuretic neurohypophysial hormone) had no effect on fowl coprodeal-colonic Na^+ and K^+ transport at doses giving "very moderate" antidiuresis (Skadhauge, 1967), but the trial was very small (2 birds). There has been no systematic study of antidiuretic hormone effects on bird intestines.

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SYMPOSIUM ON
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Seasonal and Geographic Variation in Avian Standard Metabolic Rate

Wesley W. Weathers

Introduction

Early analyses of avian metabolism correlated standard metabolic rate (SMR) with mass and taxonomic affinity. Subsequently other factors were discovered to influence SMR including time of day, and length of time in captivity (Pohl, 1969; Aschoff & Pohl, 1970; Pohl, 1977). Avian SMR also varies with season in a mass dependent manner, and with geographical location in a manner which reflects global variation in climate. This can be illustrated using data from studies in which SMR was determined on fasting birds at rest in the dark, under thermoneutral conditions, by open flow measurements of gas exchange.

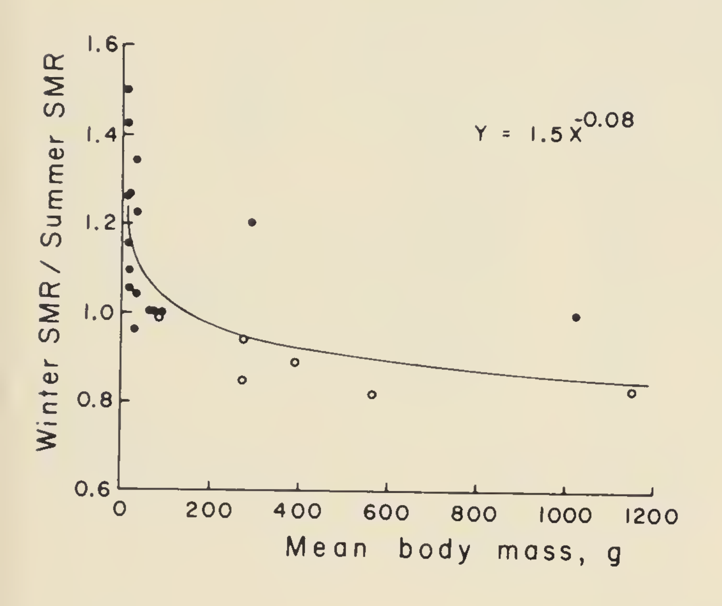


Figure 1. Relation of the ratio of standard metabolic rate (SMR) measured in winter and summer to body mass in birds seasonally acclimatized out of doors. Circles represent non-passerines, dots passerines. Coefficient of correlation for power fit curve is 0.71 ($P < 0.01$).

Seasonal variation

Considerable attention has been given to the effect of season on avian metabolism (for review see Dawson & Carey, 1976). While several different approaches to this problem have been employed, in 15 studies SMR was determined (on a total of 20 species) during both winter and summer on birds which were acclimatized out of doors to the natural seasonal variation in weather (Riddle et al., 1934; Wallgren, 1954; Irving et al., 1955; Hart, 1962; Veghte, 1964; Gelineo, 1969; Hissa & Palokangas, 1970; Davydov, 1971; Pohl, 1971; Southwick, 1971; West, 1972; Pohl & West, 1973; Rising & Hudson, 1974; Veghte, 1975; Dawson & Carey, 1976). In 8 of the previously studied species winter SMR exceeded summer SMR by 10% or more, in 4 species the converse was true, while in 8 species winter and summer SMR differed by less than 10%. Analysis of the data did not reveal any trend between seasonal variation in metabolism and latitude of occurrence, or migratory status of the birds. However, when the ratio of winter SMR to summer SMR (calculated from the above studies) is plotted against body mass, a significant correlation is obtained (Fig. 1). The increase in SMR seen in small birds in winter suggests

Department of Avian Sciences, University of California, Davis, CA, U.S.A.

that they are unable to compensate for winter conditions by increasing insulation, resorting instead to enhanced thermogenesis. Apparently this seasonal reorganization of metabolic capacity is expressed in the thermal neutral zone as well as at low temperatures (e. g., DAWSON & CAREY, 1976).

TABLE 1: Comparison of observed (obs.) and predicted* (pred.) rates of standard metabolism (SMR) in cold climate birds

Species	SMR Wkg^{-1}			Source
	Obs.	Pred.	% Δ	
Acanthis flammea†	28.4	25.0	113	WEST, 1972
Acanthis flammea†	23.6	19.8	130	POHL & WEST, 1973
Acanthis flammea	25.7	19.4	132	STEEN, 1958
Aptenodytes forsteri	1.8	2.0	90	PINSHOW et al., 1977
Aptenodytes forsteri	1.8	1.9	95	PINSHOW et al., 1976
Corvus caurinus	14.3	10.0	143	IRVING et al., 1955
Eudyptes chrysolophus	5.3	3.0	175	SCHOLANDER, 1940
Lagopus lagopus	5.9	5.2	114	WEST, 1972
Lagopus lagopus	7.3	4.3	169	WEST, 1972
Lagopus leucurus	7.3	4.8	151	JOHNSON, 1968
Larus hyperboreus	9.4	4.0	236	SCHOLANDER et al., 1950
Plectrophenax nivalis	18.1	17.9	101	SCHOLANDER et al., 1950
Pygoscelis adeliae	3.1	3.1	101	PINSHOW et al., 1977
Pygoscelis papua	5.7	2.8	205	SCHOLANDER, 1940

* By the appropriate equation of ASCHOFF & POHL, 1970. † = Mean of winter and summer values. %Δ = (observed ÷ predicted) × 100.

Geographic variation

Values of SMR for 10 species which mainly occur at latitudes exceeding 50° are presented in Table 1. In these cold climate forms SMR averages 47% higher than predicted from the birds' mass. The Emperor Penguin, *Aptenodytes forsteri.* and the Adélie Penguin, *Pygoscelis adeliae,* are conspicuous exceptions to this trend. Relatively low SMR in these two penguin species may relate to the prolonged fasts they undergo during the breeding season.

Seasonal changes in SMR can complicate analysis of geographic variations in metabolism. In the Common Redpoll *(Acanthis flammea)* SMR in winter exceeds that predicted from mass by an average of 41%(STEEN, 1958; WEST, 1972; POHL & WEST, 1973) while summer values average 98% of the predicted level (WEST, 1972; POHL & WEST, 1973). In order to take this seasonal variation into account the mean of winter and summer SMR is given for the Common Redpoll in Table 1. Most of the other species in Table 1 are large enough that seasonal variations in metabolism would not result in an elevation in SMR. Elevated SMR per se lacks adaptive value in cold climates, since SMR is by definition determined at thermoneutrality. Perhaps a correlation exists between SMR and summit metabolism such that, as with small birds in winter, increased capacity for heat production at low air temperatures involves metabolic changes which are reflected at thermoneutrality.

WEATHERS (1977) suggested that a reduced SMR may be characteristic of tropical birds. Recent further studies of tropical species require modification of this earlier suggestion. It now appears (Table 2) that while SMR is low in species which forage in the sun, it is not depressed in birds which occupy shaded habitats. Birds which forage in the sun are subject to greater heat loads than those which forage in the shade. High ambient humidity, a characteristic of tropical climates, limits the ability of animals to compensate for heat loads by increasing evaporative cooling (WEATHERS, 1977). Thus a reduced level of endogenous heat production in tropical birds which forage in the open would serve to extend the time they could be exposed to intense tropical insolation, and thus has adaptive significance.

TABLE 2: Comparison of observed (obs.) and predicted* (pred.) rates of standard metabolism (SMR) in tropical birds

Species	SMR Wkg^{-1}			Source
	Obs.	Pred.	% Δ	
Forage in Shade				
Manacus vitellinus	17.5	16.9	103	VLECK & VLECK, unpubl. obs.
Pipra mentalis	25.8	21.7	121	SCHOLANDER et al., 1950
Pipra mentalis	20.7	17.9	116	VLECK & VLECK, unpubl. obs.
Thamnophilus punctatus	16.2	16.2	100	VLECK & VLECK, unpubl. obs.
Trogon rufus	9.8	7.7	98	YARBROUGH, 1971
Vestiaria coccinea	20.6	22.9	90	MACMILLEN & CARPENTER, 1977
Forage in Sun				
Colius striatus minor	6.5	9.6	68	BARTHOLOMEW & TROST, 1970
Estrilda troglodytes	19.7	31.1	64	LASIEWSKI et al., 1964
Leptotila verreauxi	6.8	6.1	111	VLECK & VLECK, unpubl. obs.
Lonchura fuscans	10.5	20.0	51	WEATHERS, 1977
Uraeginthus bengalis	17.3	28.4	59	LASIEWSKI et al., 1964
Vidua paradisea	18.1	6.7	70	TERROINE & TAUTMANN, 1927
Xiphorhynchus guttatus	10.0	13.1	76	VLECK & VLECK, unpubl. obs.

* By the appropriate equation of ASCHOFF & POHL, 1970. %Δ = (observed ÷ predicted) × 100.

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Patterns of Energy Use in Birds

F. Reed Hainsworth

Introduction

Ecological energetics has traditionally emphasized energetics (primarily expenditures) with little input from ecology. This may be partly due to lack of information needed to test ecological ideas. If this is the case we should attempt to identify the ideas, systems, and approaches needed to supply necessary information.

Ideas

Several ecological theories involving energetics concern "optimal feeding" or resource use (see Rapport & Turner, 1977). They presume an organism's relative ability to survive and reproduce is related to feeding "efficiency" defined as net food intake value per unit time (rate of net energy and/or nutrient gain). To examine these and other theories information is needed to account for both expenditures and intakes of energy in traditional economic terms.

System

Rates of net energy gain can be studied for hummingbirds in the laboratory. Expenditures can be estimated from time budgets, and intakes from sugar water (Hainsworth et al., 1977). The ease with which both expenditures and intakes can be placed in an ecological context makes this system useful for examining ecological ideas (Hainsworth & Wolf, 1979).

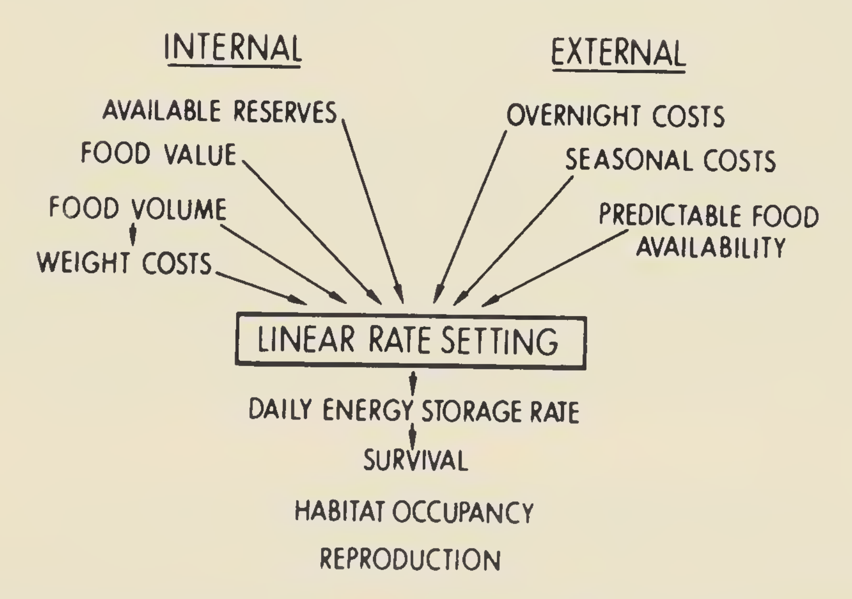


Figure 1. General summary of factors influencing energy storage rates for hummingbirds. See text for explanations.

Approach

Even with the ability to account for expenditures and intakes, the longer the interval the greater the technical difficulties of analysis. The usual period for study has been 24 hrs

Department of Biology, Syracuse University, Syracuse, New York, U.S.A.

(e. g., Wolf, 1975). But perhaps problems could be initially minimized by identifying the shortest intervals for energy regulation. Patterns of energy use over longer periods could then be studied by extending analysis of the mechanisms operating over short intervals.

The shortest possible interval for energy regulation is from one meal to the next. Hummingbirds (Wolf & Hainsworth, 1977) and rats (LeMagnen, 1975) expend energy from a meal prior to initiating the next meal with some energy diverted for longer-term storage. The sum of net gains from one meal to the next within and among days will provide for periods when expenditures exceed intakes (overnight, migration, reproduction). It is of interest to examine possible mechanisms for and determinants of rates of net energy gain since they should influence survival and reproduction. Figure 1 summarizes some factors influencing daily rates of energy storage that will be discussed below.

Determinants of energy storage rates

Energy storage will depend on meal initiation relative to consumption. Food is initially stored in a holding organ (a crop for hummingbirds), and mechanisms of energy storage have been interpreted relative to their possible function. For example, hummingbirds store less energy after small meals perhaps due to threshold detection for meal initiation relative to an exponential crop emptying rate (Wolf & Hainsworth, 1977). They also can store less energy from very large meals perhaps due to costs associated with the weight of a meal (DeBenedictis et al., 1978). Since energy storage rates depend on quantity consumed, meal size could reflect some maximum rate of net energy gain. Recent studies indicate that the characteristic meal sizes of hummingbirds may result in optimal rates of energy storage (DeBenedictis et al., 1978; Hainsworth, 1979).

In addition to volume, crop function may be also influenced by feedback mechanisms related to food energy value. Food of lower value may empty faster for a given level of expenditure. If the crop emptied in direct proportion to energy value then energy storage rates would be similar as food concentration changed. However, the rate constant for crop emptying may not decrease in direct proportion as food value increases. This would produce higher rates of energy storage as food value increased, and energy budget studies indicate this (Wolf & Hainsworth, 1977). Optimal feeding theories suggest that a rate of energy storage dependent on food value should produce food selection based on value. Food selection by hummingbirds is strongly influenced by sugar concentration (Hainsworth & Wolf, 1976), and this may reflect the relative impact of concentration on energy storage rates.

Some theories suggest energy accumulation rates should be "maximized" (e. g., Ellis et al., 1976), but unconstrained maximization could lead to obesity. Removing the constraint of food availability in the laboratory indicates rates of energy storage are not necessarily at a uniform "maximum" (see below). Energy storage rates may be limited by internal and external factors, and it is important to determine their impact.

An alternative to absolute maximization would be to have energy storage rates adjustable and maximized with respect to demands. Demands could be set by periods when expenditures exceed short-term intake. Tests of this hypothesis require identifying costs associated with various intervals, and once again, longer (seasonal) intervals present the greatest difficulties so perhaps we should also examine shorter periods. For many

organisms this will be the portion of a day when feeding does not occur, and KENDEIGH et al. (1969) suggested daily energy accumulation in two species of granivorous birds was determined by prior night energy expenditures. Other studies of fat deposition by birds suggested a similar pattern (NEWTON, 1969; EVANS, 1969).

We measured daily net energy gains for hummingbirds together with energy expenditures the previous night (Fig. 2). This suggests a relationship, although mean rate of net energy gain differs considerably from predicted values. Thus, other factors besides overnight expenditures may influence storage rates. One candidate could be the level of available reserves. If organisms could integrate information on anticipated required expenditures with levels of available energy storage they could perhaps precisely regulate energy over relatively long periods.

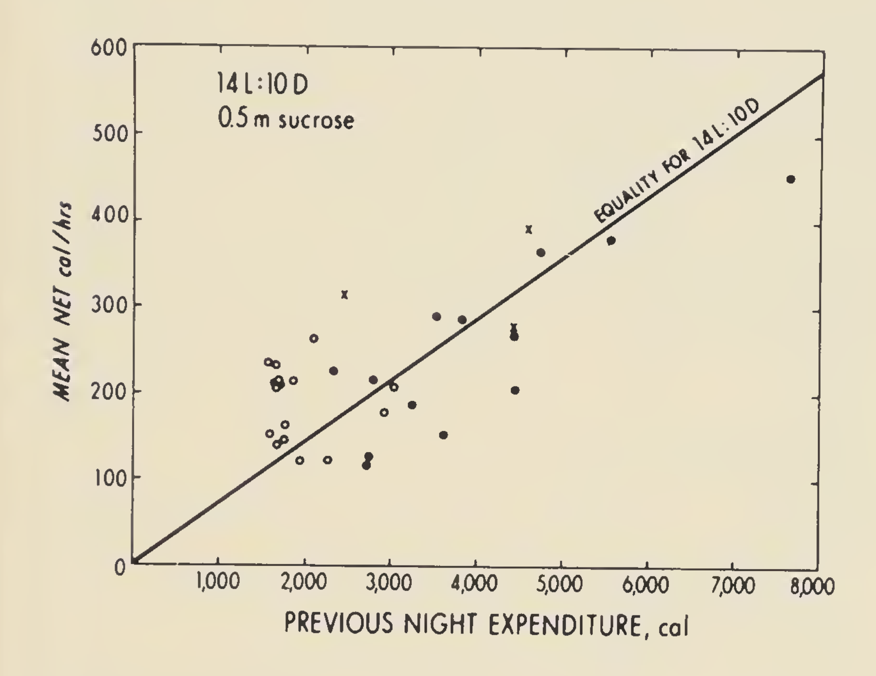


FIGURE 2. Mean rate of energy storage *vs* overnight expenditures measured from oxygen consumption. Each point is a separate determination. Equality line assumes constant rate of storage throughout a day. ● = male *Eugenes fulgens*, o = female *A. alexandri* x = female *Lampornis clemenciae*.

Under this hypothesis organisms with low energy reserves may accumulate at rates greater than predicted while those with high energy reserves may accumulate at rates lower than predicted. An important concern is to quantify high and low reserves. A sufficient level of energy reserve probably varies, and until it is defined it will be difficult to test the hypothesis. However, it is possible to examine energy storage responses to extreme energy reserve depletion, and by manipulating reserves on a short-term basis we can begin to ask if and how some organisms monitor levels of energy reserves.

Measurements of energy storage rates

We studied rates of net energy gain for four female *Archilochus alexandri* fed 0.5M sucrose and deprived of food either from a photoperiod change (14L to 9L, Fig. 3, 1–4) or from 2–3 hr food deprivation during the day (Fig. 3, 5–6). The rate of energy storage was remarkably linear within a day. There generally was little change following deprivation during the day except for the first half-hour of returned access to food. However, rates of energy storage were increased the day following deprivation in 3 of 4 cases. Increases in energy storage rates from day to day appeared to occur either from an increase for the first half-hour or from a sustained increase (Fig. 3). Sustained adjustments appeared to occur

within the first few days following torpor (Fig. 3). This was predicted since hummingbirds only enter torpor when energy reserves have been depleted to some minimum threshold (HAINSWORTH et al., 1977). However, torpor was not necessary to cause an increase in rate of energy storage (Fig. 3).

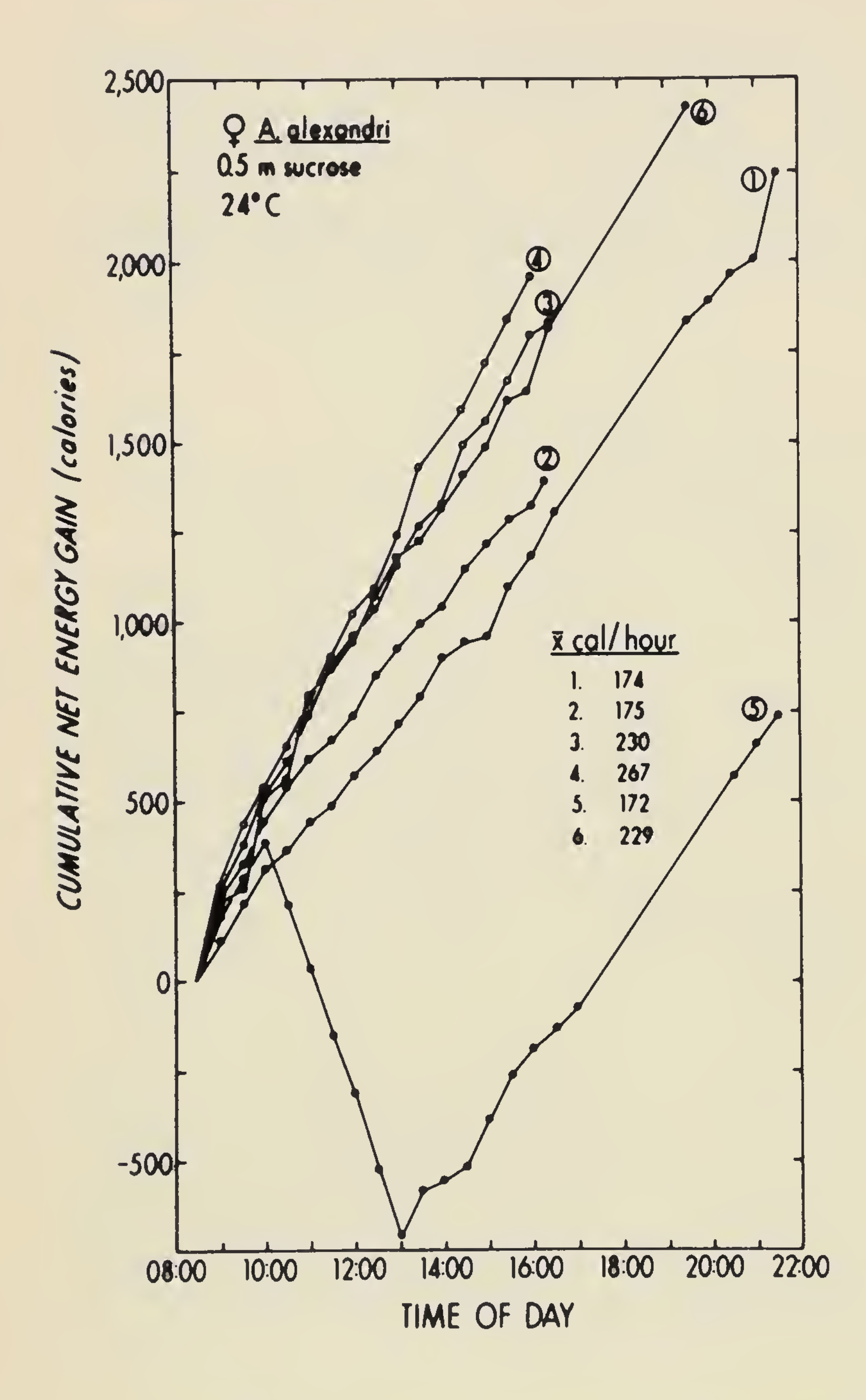


FIGURE 3. Cumulative energy storage for a female *A. alexandri* fed 0.5M sucrose. Numbers 1–4 represent successive days with a 14L to 9L photoperiod change. Torpor occurred the nights preceding days 3 and 4. Numbers 5–6 represent 3 hrs deprivation with the subsequent day.

There appear to be limits on rates of energy storage. The rate can increase or decrease from day to day, but the range for *A. alexandri* fed 0.5M sucrose was between 150–350 cal/hr. The upper limit may be set internally, perhaps as a consequence of crop or digestive function. The range of adjustments with respect to changing demands with 0.5M sucrose was similar to rate changes that occurred between different food concentrations when demands were similar. This further emphasizes the importance of food selection for optimal feeding behavior.

The constancy of energy storage rates in hummingbirds has been proposed to be due to a compromise between costs associated with weight and predictable access to food (WOLF & HAINSWORTH, 1977). An initially rapid rate of storage followed by maintenance could

increase costs for maintenance due to added weight. Delay of gains until late in the day would require highly predictable access to food.

The constancy of rate of energy storage in hummingbirds within a day suggests the rate may be "set" on a daily basis (Fig. 1) in contrast to a variable rate resulting in some required level of energy storage prior to nightfall. The rate may be set from a comparison of overnight expenditures with levels of energy reserves within limits set by maximum rate capacity and food value rate determinants.

Patterns and determinants of energy storage have important implications for ecological interpretations. The absolute values can provide a basis for interpreting aspects of resource use based on relative rates of energy storage and also to infer some characteristics of the interaction between an organism and its environment. For example, a maximum limit for rate of energy storage could determine the minimum daylight period to accumulate overnight energy requirements. The minimum time would increase as overnight costs increased. For a 3.3 g *A. alexandri* a maximum storage rate of 350 cal/hr coupled with overnight costs from temperature dependent standard metabolic rate (from HAINSWORTH & WOLF, 1978) would dictate a doubling of minimum required daylight time (from 6 to 12 hrs) as environmental temperature overnight decreased from 27 to 0°C. This could limit seasonal distribution independent of resource availability. Other costs associated with molt, reproduction, or migration would set additional limits which could be ameliorated by anticipatory energy storage.

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Energetics of Foraging and Free Existence in Birds

David M. Bryant and Klaas R. Westerterp

Introduction

The energy requirements of a bird must be obtained by foraging. This paper examines foraging rates for a wide range of birds and compares these data with their energy requirements. We then examine the relationship between energy income and the costs of feeding (the ratio hereafter called foraging efficiency) for one foraging guild, aerial feeding birds, and discuss the life history consequences of interspecific differences. Finally data are presented on individual variability in daily energy expenditure for one member of this guild, the House Martin, *Delichon urbica,* and its significance for the energy costs of foraging and breeding are discussed.

Foraging rates in birds

Foraging rates (F_r, energy intake or capture rates in $kJ.h^{-1}$) have been calculated from published data on birds observed feeding in the wild. Data for conditions of food scarcity or when feeding was affected by special circumstances (such as bringing very small items to hatchlings) have been excluded from the analysis. This leaves data for birds either feeding their young (inevitably including a time component for travel in some studies) or self-feeding at various times of year. Foraging rate is described by the allometric equation: $F_r = a W^b$ where W is body weight (g) and *a* and *b* are constants (Fig. 1). For all species combined, except seabirds for which the data are inconsistent, the value of the exponent *b* is 0.68 (Table 1). For individual guilds however the exponent generally lies close to or exceeds unity. Thus because empirical values of daily energy expenditure (DEE) in birds range from $W^{0.50}$ to $W^{0.71}$ (King 1974, Kendeigh et al. 1977), within foraging guilds, larger size leads to an increased rate of energy gain. This advantage for larger birds is

Table 1: Coefficients of allometry for foraging rates (F_r $kJ.^{-1}$) in relation to body weight (Wg) in birds ($F_r = aW^b$).

Foraging guild	Coefficient a	Coefficient b	Sample size	F. for 100 g bird
All species	2.16	0.64*	67	41.65
All species (less seabirds)	2.02	0.68*	55	46.10
Wildfowl	1.79	0.67	3	38.66
Raptors	0.26	1.04*	9	32.15
Shorebirds	0.04	1.26*	15	12.71
Nectarivores	1.42	1.09*	6	(210.86)
Passerines	0.92	0.94	14	68.58
Aerial feeders	2.33	0.56	8	30.45
Seabirds	16.33	0.19	12	38.44

(* = significance of slope $p < 0.01$)

Department of Biology, University of Stirling, Stirling, Scotland, U.K.

unlikely to be reduced when the energy costs of foraging alone are considered since the relative energy costs of travel ($kJ.g.^{-1}\ km^{-1}$) decrease with size (TUCKER 1970, SCHMIDT-NIELSEN 1972). For comparing the effect of food type on rates of energy gain it is useful to examine F_r for a notional 100 g bird in each guild. F_r ranges from a low level of 12.7 kJh^{-1} among shorebirds to 210.9 $kJ.h^{-1}$ among nectarivores. The predicted value for

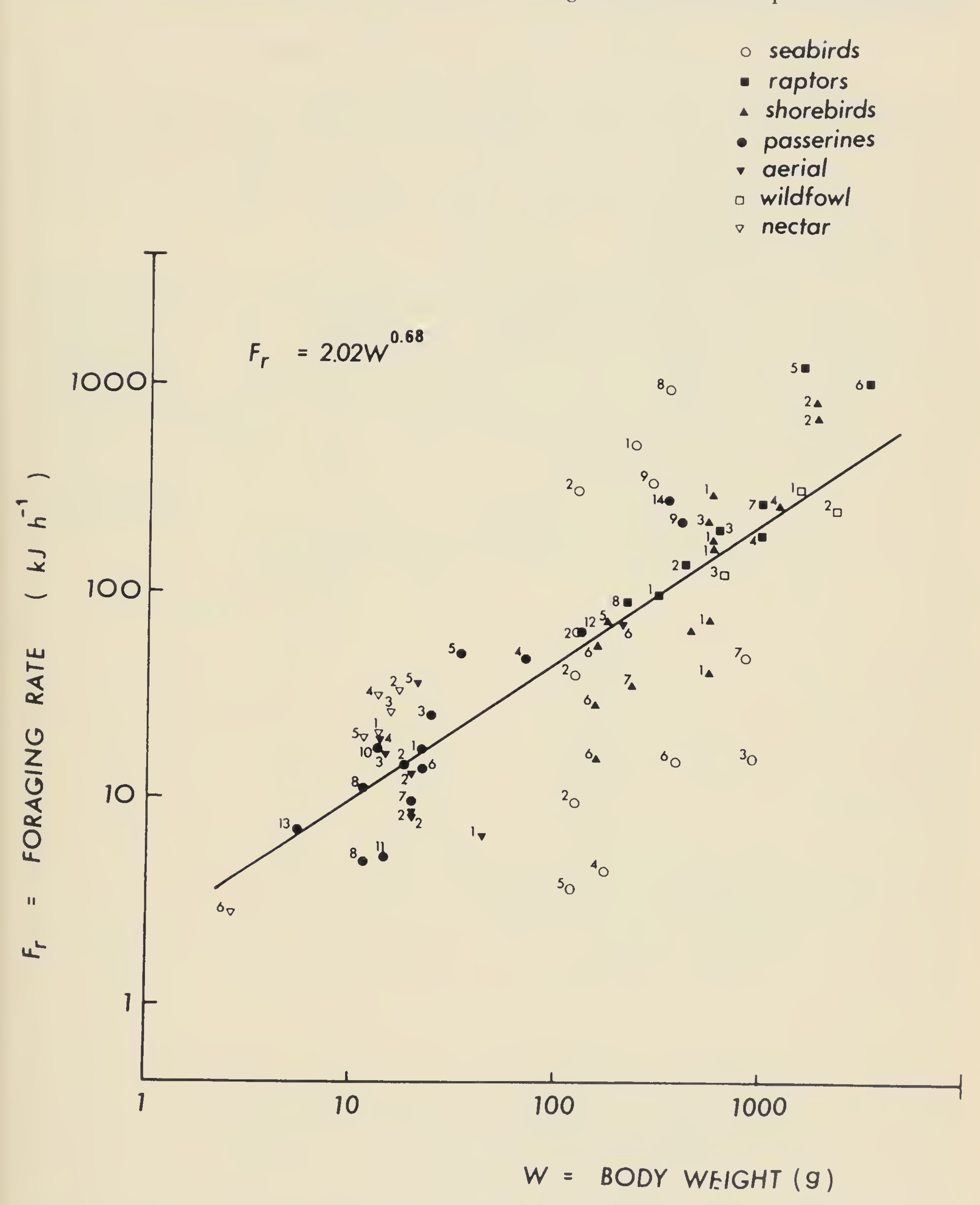


FIGURE 1. The relationship between foraging rate (F_r, energy intake rate) and body weights in birds. The fitted line is for all species (except seabirds); see Table 1. Energy value of food items was calculated from data of CUMMINGS & WUYDCHECK (1971) and DRIVER, SUDGEN & KOVACK (1974) if not available in the original paper. The identity of each point is given in the Appendix.

nectar feeders however clearly extends beyond the range of the data and perhaps a more significant upper limit is that for the passerine guild which is 68.6 kJh^{-1}. Within the guild of aerial feeding birds there was no consistent trend with body weight. We therefore present an analysis of energy income and costs among aerial feeders and examine the significance for their life histories.

Foraging efficiency in aerial feeding birds.

Hirundines and swifts take virtually all their insect food in the air. Foraging costs can therefore be estimated crudely from a knowledge of the costs of flight. Flight costs for aerial feeders are available from several sources and yield remarkably consistent results. They invariably show less than half the energy expenditure for flight of other species matched for size. (Hails 1977).

Data for foraging rates in four species (Swift, *Apus apus;* House Martin; Sand Martin, *Riparia riparia;* Swallow, *Hirundo rustica)* have been obtained by direct observation at the nest for Swifts (Lack 1956) and similarly for other species by the authors and D. R. Waugh, A. K. Turner and C. J. Hails. By restricting measurements to bouts of feeding the young, for the hirundines the problem of parental self-feeding being additional to the insects in the bolus is minimised. This factor however remains a difficulty for the Swift, thereby probably yielding a marginal underestimate of foraging rate.

Table 2: Foraging rate F_r in $kJ.h^{-1}$), mean flight metabolism (M_f in $kJ.g^{-1}h^{-1}$), and foraging efficiency ($F_{eff} = f_r/M_f$) for four aerial feeding birds.

Species	F_r	M_f*	Body Weight (g)	F_{eff}**
Swift *Apus apus*	6.35	0.17	42.5	0.92
House Martin *Delichon urbica*	8.25	0.19	19.4	2.24
Swallow *Hirundo rustica*	36.26	0.26	20.2	6.81
Sand Martin *Riparia riparia*	22.65	0.23	13.7	7.06

* The following sources have been used in these calculations: Dolnik & Gavrilov (1971), Lyuleeva (1970), Kespaik (1968), Hails (1977), Potapov (1971), Oehme (1968), Pennycuick (1975).

** Clearly the Swift cannot survive with a mean F_{eff} of less than one. If it is assumed to delivering food to the young, $E_{eff} = 2.35$. Similar calculations yield for *D. urbica,* 3.67; *H. rustica,* 8.29 and *R. riparia,* 8.50.

On an interspecific basis foraging efficiency can be arranged in a hierarchy with the Swift at the bottom and Sand Martin at the top (Table 2). This sequence shows striking parallels with aspects of the life history and structural attributes of these species (Table 3). The species with the highest foraging efficiencies (Sand Martin and Swallow) arrive early when aerial food is scarce, breed earliest and rear the largest broods. The wing loading and manouverability are also matched to the sequence of foraging efficiencies. Although for data of this type it is not possible to segregate cause and effect, a simple explanation is that the structural attributes of each species confer upon them a specific range of foraging efficiencies which, for individuals of each species trying to maximise fitness, leads to the

observed sequence of breeding output: the most rapid foragers having the greatest outputs. This view relies on foraging costs being a relatively static component of the efficiency of foraging and implies that the changes in efficiency which facilitate the start of breeding and bring about the seasonal decline in clutch size are predominantly a function of seasonal changes in resource abundance (BRYANT 1975). As stated above however the topic of variability in breeding costs, mainly due to the costs of foraging for the brood at different seasons and under different conditions, remains to be investigated in detail.

TABLE 3: Life history parameters, structural attributes and energetics data for four aerial feeding birds.

	Swift *Apus apus*	House Martin *Delichon urbica*	Swallow *Hirundo rustica*	Sand Martin *Riparia riparia*
Main arrival time	late May	early May	mid April	early April
Begin laying	late May	mid May	late April	late April
1st clutch size	2–3	3–5	4–6	4–6
% 2nd clutches	nil	87	67–92	60–90
2nd clutch size	—	2–4	3–4	3–4
Wing loading $g.cm^{-2}$	3.86	4.74	6.11	5.03
Manouverability Index (Tail length mm/ body weight, g)	1.8	3.1	5.2	3.9
Foraging efficiency range	0.92–2.35	2.24–3.67	6.81–8.29	7.06–8.50

Energetics of foraging and free existence in breeding House Martins

Monitoring energy expenditure of breeding House Martins using the doubly labelled water technique (LIFSON et al. 1955), HAILS (1977) identified two significant causes of variation in daily energy expenditure. Firstly, for males, expenditure increased with brood mass although there was no comparable trend for females. This difference was matched to the sexual differences in feeding response to brood mass because females tended to feed at a fixed rate with the residual nestling demand being taken up by the male. Thus the larger or heavier the brood the more time the males were required to forage. The same trend was apparent when broods were artificially enlarged except in one case where some of the brood died. This result paralleled that of UTTER & LEFEBVRE (1973) for Purple Martins *Progne subis* where they suggested that the sexual differences in energy expenditure arose from differences in time spent feeding the brood. Secondly HAILS (1977) was able to show that the expenditure for the pair in rearing a second brood of the overall average size was 30′ higher than for first broods, the increase being shared equally between the sexes.

In neither of these studies was it possible to identify the fate of the energy expended by reference to the experimental individuals' time and activity budgets. With this in view the present study was undertaken, involving simultaneous time budgets and measurement of energy expenditure by the $D_2 O_{18}$ method for individuals of known age. We report here our results for eight birds which were feeding nestlings of 12–16 days over a two day period. At the start and end of a run the birds were weighed and their fat reserves scored. A parallel study of fat scores and the fat content of carcasses yielded data which allowed calculation of changes in fat content during each run.

TABLE 4: Mean energy expenditure and time budget data for breeding House Martins with their age (all with a brood of four young of about 14 days monitored for two days).

Nest	Sex	Age (yrs)	Energy expenditure ($kJ.g^{-1}.h^{-1}$)	Time in Flight (%)
1	♂	3	0.206	49.1
1	♀	2	0.310	50.3
2	♂	2	0.318	52.5
2	♀	3	0.203	33.4
3	♀	1	0.440	46.4
4	♂	1	0.394	58.7
5	♂	3	0.160	44.1
5	♀	2	0.348	52.2

There was a twofold difference between the lowest and highest levels of energy expenditure (Table 4). The differences among the 8 birds however could not be explained in terms of the time spent in flight or other indices of activity such as feeding rate at the nest, nor by environmental factors. The birds differed in their tendency to subsidize foraging activity by drawing on their fat reserve (Fig. 2). This tendency was closely linked to parental age, older birds using more of their fat and hence expending the least energy ($r = -0.97$, $p < 0.01$). Presumably the significance of age for predicting which birds make the greatest use of energy reserves to subsidize foraging is related to age-specific differences in reproductive strategy (FISHER 1930, WILLIAMS 1966, PIANKA & PARKER 1975, PIANKA 1976).

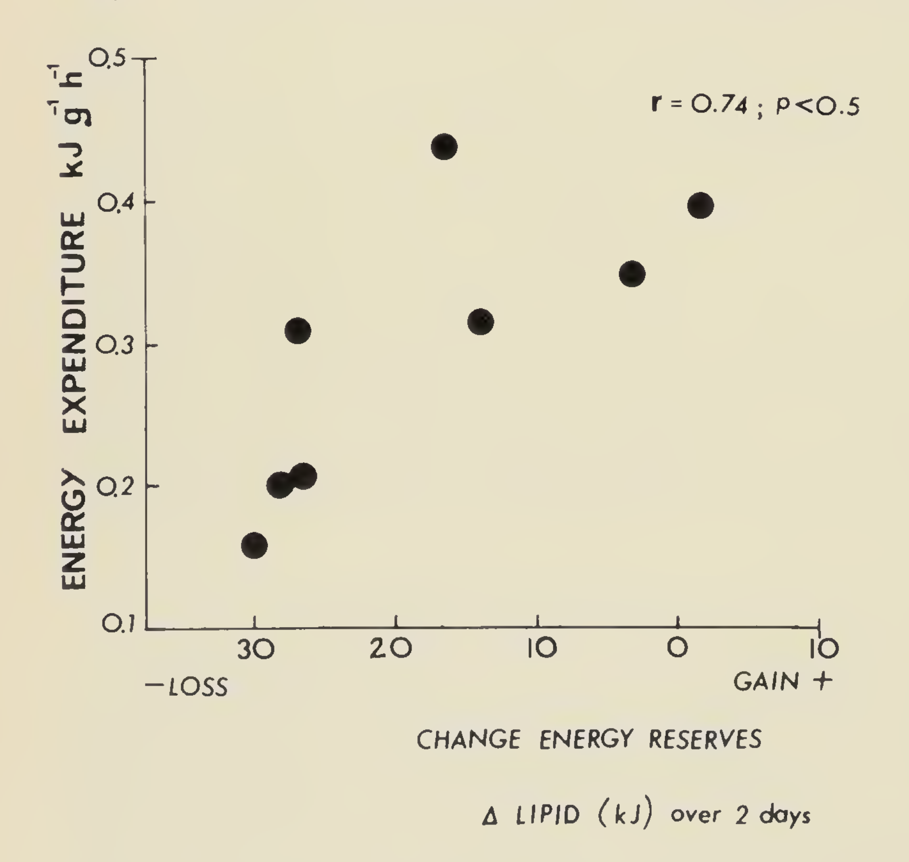


FIGURE 2. Mean energy expenditure of breeding House Martins over two days in relation to changes in the energy content of their fat reserves.

Two final points need to be made regarding the impact of energy reserves on current energy expenditure in breeding House Martins. Firstly older birds tend to establish a larger fat store at the start of breeding and thereby spread the energy costs of the necessarily high

level of foraging activity at the nestling stage. Secondly the loss of condition during their first broods prevents parents subsidizing foraging costs for second broods and this leads to higher energy expenditures on second broods (Hails 1977).

Appendix

Passerines. 1. *Fringilla coelebs* (Dolnik, 1972); 2. *Motacilla flava,* 3. *Motacilla alba* (Davies, 1977). 4. *Sturnus vulgaris* (East & Pottinger, 1975); 5. *Spiza americana* (Schartz & Zimmerman, 1971); 5. *Anthus spinoletta* (Gibb, 1956); 7. *Parus major* (Royama, 1966); 8. *Parus caeruleus* (Royama, 1966, Krebs, 1970); 9. *Corvus frugilegus* (Feare et al. 1974); 10. *Acrocephalus schoenobaenus* (Bibby et al. 1976); 11. *Muscicapa striata* (Davies, 1977); 12. *Zenaidura macroura* (Schmid, 1965) (included in passerine guild); 13. *Regulus regulus* (Gibb, 1960); 14. *Bubulcus ibis* (Siegfried, 1972) (not included in passerine guild equation).

Raptors. 1. *Circus pygargus,* 2. *C. cyaneus,* 3. *C. aeruginosus,* (Schipper, 1973); 4. *Buteo galapagoensis,* (Vries, 1976); 5. *Pandion haliaetus* (Green, 1976); 6. *Aquila verreauxii* (Gargett, 1972); 7. *Buteo buteo* (Dare, 1971); 8. *Falco tinnunculus* (Cave, 1968);

Seabirds. 1. *Thalasseus sandvicensis,* 2. *Sterna hirundo* (Dunn, 1973); 3. *Uria aalge* (Birkhead, 1976); 2. *Sterna hirundo* (Nisbet, 1973, 1977); 4. *Sterna fuscata,* 5. *Anous stolidus* (Brown, 1975); 6. *Fratercula arctica* (Corkhill, 1973); 7. *Larus argentatus* (Spaans, 1971); 2 *Sterna hirundo,* 8. *Sterna maxima,* 9. *Rynchops nigra* (Erwin, 1977);

Shorebirds. 1. *Haematopus ostralegus* (Brown & O'Connor, 1974); 2. *Ardea herodias, A. occidentalis,* 3. *Florida caerula,* 4. *Casmerodius egretta* (Recker & Recker, 1968); 1. *H. ostralegus* (Heppleston, 1971, Davidson, 1967, Drinnan, 1958, Hulscher, 1976, Goss-Custard, (1977); 5. *Pluvialis apricaria* (Bengston, 1976); 2. *Ardea herodias* (Krebs, 1975); 6. *Tringa totanus* (Goss Custard, 1977 a & b, J. Warnes, unpubl); 7. *Calidris canutus* (Prater, 1972);

Wildfowl. 1. *Branta leucopsis* (Ebbinge, et al. 1975); 2. *Anser albifrons* (Owen, 1972, 1976); 3. *Oxyura maccoa* (Siegfried et al., 1976);

Aerial. 1. *Apus apus* (Lack, 1956); 2. *Delichon urbica* (Gunten & Schwartzenback, 1962, Hails, 1977, Bryant, unpubl); 3. *Iridoprocne albilinea* (Ricklefs, 1971, 1974); 4. *Riparia riparia* (Waugh & Turner, unpubl.); 5. *Hirundo rustica* (Waugh & Turner unpubl.); 6. *Falco subbuteo* (Thiollay, 1967) (also included in raptors).

Nectarivores. 1. *Nectarinia famosa* (Wolf, 1975); 2. *Nectarinia kilimensis,* 3. *N. senegalensis,* 4. *N. reichenowi,* 5. *N. mariquensis,* (Gill & Wolf, 1975); *Selasphorus flammula,* (Hainsworth & Wolf, 1972);

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Energy Expenditure in Free-living Birds: Patterns and Diversity

Glenn E. Walsberg

Introduction

The energetics of birds, as of other taxa, has necessarily been studied primarily in the laboratory. In an ecological sense, the results of such analyses may be regarded as artifacts (albeit, artifacts of fundamental value) since they reflect the animal's interaction with an artificial environment. Estimating the energy metabolism of a bird in its natural setting over a prolonged period (e.g., a daily cycle) is a complex task, however, since power consumption at this level of integration is the product of a multitude of biotic and abiotic factors (see King's [1974] Figure 1). Though still primitive, our knowledge of the importance and operation of these diverse factors has advanced substantially in recent years and, with increasing frequency, this has stimulated attempts to estimate the daily energy expenditure (DEE) of free-living birds. Limited space does not permit discussion of the extraordinary variety of methods that have been used to estimate daily power consumption (see reviews by Gessaman, 1973; King 1974; Kendeigh et al., 1977). Data in the present review are derived from all methods except those based primarily upon analyses of captive birds and extrapolated to the natural state without considering behavioral differences between the caged and free-living animal. This is not an arbitrary exclusion since it will be shown that behavioral adjustments are of major importance in determining variation of power consumption in nature.

As is to be expected in a relatively new and rapidly expanding field, estimates of DEE vary greatly in their apparent reliability. In spite of the uncertainties of particular estimates, however, it is possible to discern a number of recurring patterns that are the subject of this review.

Daily energy expenditure as a function of body mass

DEE does not closely parallel basal metabolism as a function of body mass; rather it varies substantially between its approximate upper limit (power consumed in 24 h of flight) and its lower limit (basal metabolism). A least-squares regression of DEE (kJ/day) on body mass (g) for the total data pool (ignoring heterogeneous methods, averaging multiple estimates for species, using median values when estimates for various phases of the annual cycle are reported, and averaging body mass for sexually dimorphic species) yields the equation

$$\log DEE = \log 11.87 + 0.608 \log W \qquad (1)$$

where $n = 30$, $S_{\log}\, y_{\cdot \log}\, X = 0.0997$, and $r = 0.970$. Separate regression equations for passerines and nonpasserines are not statistically distinguishable, and inspection of Figure 1 reveals no obvious passerine/nonpasserine disparity like that of the basal metabolic rate (BMR).

The 0.61 slope of equation 1 differs substantially from the 0.73 slope of the equations describing flight metabolism and maintenance metabolism. Since these two factors are

Department of Zoology, Washington State University. Pullman, Washington, U.S.A.

major components of total daily energy expenditure, one would also expect DEE to have a similar relation to body size if the proportions of energy allocated to these categories are relatively independent of body size. This assumption is not realistic since smaller birds tend to be more intensely active than larger ones. Thus, equation 1 predicts average values of DEE equal to 2.8 x passerine BMR for a 10-g bird and only 1.7 x passerine BMR for a 1000-g bird. Birds that forage on the wing are a distinct class hardly overlapping in DEE

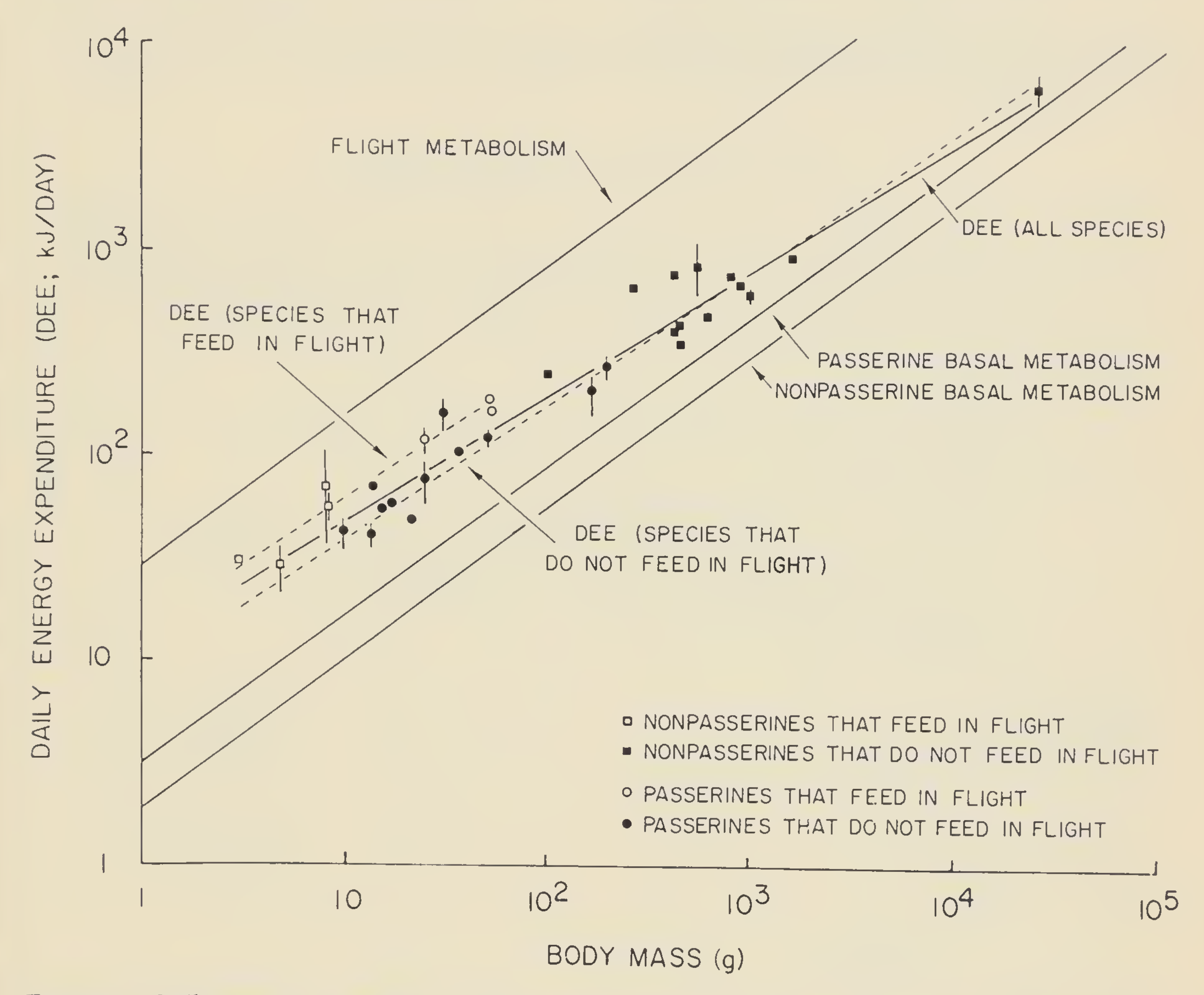


FIGURE 1. Daily energy expenditure (DEE) as a function of body mass. Squares or circles represent mean or median values; vertical lines show range. Flight metabolism is calculated by the equation of HART & BERGER (1972). Basal metabolism is calculated for the rest phase of the daily cycle using the equations of ASCHOFF & POHL (1970). See text for calculation of other regression lines.

Unfilled squares (from left to right): *Stellula calliope* (CALDER, 1971), *Calypte anna* (PEARSON, 1954; CALDER, 1971, 1975, STILES, 1971; EWALD & CARPENTER, 1978), *Oreotrochilus estella* (CARPENTER, 1976), *Colibri coruscans* (HAINSWORTH, 1977).

Filled squares (from left to right): *Aegolius acadicus* (GRABER, 1962), *Asio otus* (GRABER, 1962), *Lagopus leucurus* (MOSS, 1973), *Asio flammeus* (GRABER, 1962), *Lagopus mutus* (MOSS, 1973, 1977), *Fulica americana* (MURDOCK, 1975), *Oxyura maccoa* (SIEGFRIED et al., 1976), *Eudocimus albus* (KUSHLAN, 1977), *Anas strepera* (DWYER, 1975), *Branta leucopsis* (EBBINGE et al., 1975), *Aptenodytes forsteri* (LE MAHO et al., 1976).

Unfilled circles (from left to right): *Petrochelidon pyrrhonota* (WITHERS, 1977), *Progne subis* (female and male; UTTER & LEFEBVRE, 1973).

Filled circles (from left to right): *Dendroica caerulescens* (BLACK, 1975), *Empidonax traillii* (MARXUACH, 1978), *Nectarinia famosa* (WOLF, 1975), *Nectarinia reichenowi* (GILL & WOLF, 1975), *Vestiaria coccinea* (CARPENTER & MACMILLEN, 1976), *Anthus spinoletta* (GIBB, 1956), *Phainopepla nitens* (WALSBERG, 1977, 1978), *Calcarius lapponicus* (CUSTER, 1974), *Spiza americana* (SCHARTZ & ZIMMERMANN, 1971), *Mimus polyglottos* (UTTER, 1971), *Pica pica* (female and male; MUGAAS, 1976).

with species that do not forage on the wing. Analyzing only the data for species that forage in flight yields the equation

$$\log DEE = 13.64 + 0.663 \log W \quad (2)$$

where units are as in equation 1, $n = 6$, $S_{\log Y \cdot \log X} = 0.066$, and $r = 0.977$. The data for the remaining species yield the relation

$$\log DEE = \log 8.96 + 0.653 \log W \quad (3)$$

where $n = 24$, $S_{\log Y \cdot \log X} = 0.134$, and $r = 0.973$. The lines described by these two equations are almost parallel, with the power consumption of birds that forage in flight averaging about 52% greater than that of other species.

Energy expenditure during breeding

Table 1 summarizes data on relative energy expenditure during different phases of the breeding cycle. The data have been normalized by expressing energy expenditure as a percentage of that occurring during the incubation period, which was chosen as a reference level since it is the period most frequently analyzed in different studies.

Table 1: Variation in energy expenditure during the breeding period.

	Percentage difference from daily energy expenditure during incubation		Reference
	Prebreeding period	Nestling period	
For sex that incubates:			
Calypte anna	–	+14	Calder, 1975
Empidonax traillii	–	+11	Marxuach, 1978
Petrochelidon pyrrhonota	–	+11	Withers, 1977
Pica pica	+49	+45	Mugaas, 1976
Phainopepla nitens	+ 1	+25	Walsberg, 1977, 1978
Dendroica caerulescens	− 2	+15	Black, 1975
Calcarius lapponicus	+ 6	− 9	Custer, 1974
For sex that does not incubate:			
Pica pica	− 2	+14	Mugaas, 1976
Mimus polyglottos	− 9	− 5	Utter, 1971
Dendroica caerulescens	− 2	+14	Black, 1975

In almost all species studied, DEE during the nestling period is the highest measured, typically being 10–45% above that during incubation. In contrast, available data indicate that the incubation period is energetically conservative compared to either the prebreeding or the nestling periods. The low energy expenditure during incubation is primarily a result of decreased activity due to the long periods that the parent spends on the nest. For example, time-budget data for 4 species in Table 1 *(Pica, Phainopepla, Calcarius, Dendroica)* indicate that incubating individuals spend an average of 26–90% less time in flight per day than they did during the prebreeding period. The energy requirement of actually occupying the nest and supplying heat to the eggs is controversial (see discussions by Kendeigh, 1973; King, 1973, 1974; Ricklefs, 1974; Walsberg & King, 1978 and in

press). Some authors have estimated that incubation entails an increase in resting energy expenditure of approximately 0.2 – 0.4 x BMR (e.g., BLACK, 1975) while others have estimated a decrease of similar size (WALSBERG & KING, 1978 and in press). It is apparent, however, that such relatively small shifts in energy metabolism may be of minor significance to the total energy budget of many species. For example, a constant increment or decrement of 0.3 x passerine BMR is equal to the energy expended in only about 2 minutes of flight per hour (estimated by the equation of HART & BERGER, 1972). Thus, it is likely that the energetic consequences of incubation for free-living birds are often determined primarily by the dramatic decrease of activity during this phase.

Annual patterns of energy expenditure

The elucidation of annual patterns of energy expenditure represents one of the potentially most valuable perspectives from which to evaluate the relation of energetics to the evolution of avian life histories. Unfortunately, only a few studies have been conducted during the nonbreeding period, and hence few data are available with which to analyze annual variation in power consumption. The most extensive analysis is that of Black-billed Magpies *(Pica pica)* by MUGAAS (1976). WALSBERG's (1977, 1978) study of the Phainopepla *(Phainopepla nitens)* is less detailed, and CARPENTER (1976) presents valuable but somewhat fragmentary data for the Andean Hillstar *(Oreotrochilus estella)*. Even with such a limited data base, however, a number of general points are worth noting. First, there is substantial variation in DEE through the annual cycle in all three species. Maximum values equal about 1.6 times minima in both *Pica* & *Phainopepla*, and apparently 2.9 times the minimum in *Oreotrochilus*. Second, and contrary to what is frequently assumed, winter is not necessarily a period of relatively high energy expenditure. In only the female magpie does DEE peak during the winter. Instead the highest levels of energy expenditure typically occur when the parents are feeding young. In *Pica* & *Phainopepla*, major shifts in power consumption are almost exclusively attributed to variation in activity patterns, such as changes in territorial or foraging behavior. Variation in the thermoregulatory requirement is of lesser importance. Behavioral changes are also major factors underlying variation in DEE in *Oreotrochilus*, but the extreme annual range of DEE in this species is also a result of important thermoregulatory adaptations used extensively in winter (e.g., torpor).

Summary and conclusions

Analysis of the patterns of energy expenditure in free-living birds currently suffers from an inadequate base of reliable data. Particularly unfortunate is the infrequency of analyses such as those of UTTER & LEFEBVRE (1973) that empirically test the accuracy of field methods. In spite of these drawbacks, a number of general patterns can be tentatively identified: (1) DEE does not closely parallel basal metabolism as a function of body mass; smaller species tend to have higher DEE/BMR ratios. (2) Extant data do not suggest a passerine/nonpasserine disparity in daily energy expenditure like that of basal metabolism. (3) DEE varies substantially (60–190%) through the annual cycle in the few species for which adequate data are available. (4) DEE is generally highest in adults feeding young and is often relatively low during incubation and in winter. (5) Major shifts in power

consumption appear to result mainly from behavioral changes rather than from other factors, such as variation in the thermostatic requirement. This latter point provides a cautionary note for workers; behavioral plasticity, both proximate and evolutionary, appears to be a major determinant of phasic and interspecific variation of DEE. Because of this, extrapolations to natural conditions from the results of studies of caged birds can easily become unrealistic. Reasonably accurate assessement of DEE obviously requires the use of physiologically sound methods combined with a careful evaluation of the behavior of the free-living bird.

Acknowledgments

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Energetics of Reproduction in Birds

Raymond J. O'Connor

Introduction

In an extensive review of the energetics of avian reproduction Ricklefs (1974) summarized much of the available information as to the patterns of energy expenditure during reproduction. The present paper (presented here in extended abstract form) examines (1) some of the ecological correlates of these patterns, and (2) some related ideas that have appeared in the literature since Ricklefs wrote his review.

Energetics and the timing of breeding

Perrins (1970) argued that with seasonal food supplies some, if not indeed many, species are prevented from breeding at the optimal date because the females cannot accumulate enough energy (or possibly some essential nutrient) to produce eggs early enough to yield nestlings at the time young are most easy to feed. This idea has been confirmed experimentally for the Great Tit *Parus major* by Källender (1974) who was able to accelerate the onset of laying by supplying the hens with additional food supplies during the pre-laying period. Perrins' hypothesis also applies interspecifically, smaller passerines commencing laying earlier than large species since their lower existence energies allow them adequate surplus for daily egg formation sooner (E. K. Dunn 1976). One consequence of the hypothesis is that females roosting in well-insulated nest-boxes during the pre-laying period should have lower overnight costs and correspondingly earlier attainment of an egg production energy surplus, and this indeed seems to be the case in the Oxford Great Tit population (O'Connor, 1978d). There is thus an advantage to males of such species if they build a well-insulated nest.

The influence of egg formation patterns on the energetics of laying has been investigated by King (1973) and by Murton & Westwood (1977). Since follicle growth is approximately sigmoidal the energy requirement for egg synthesis can be approximated by a sine curve. This model shows that peak energy requirement for the clutch is equal to the energy content of a single egg and that it is reached only after p-1 days (p the period of egg formation). Murton & Westwood (1977) show that when environmental energy resources are in short supply egg size can be maintained only by increasing the time taken for the synthesis of each or by spacing the eggs of the clutch further apart. Both options are energetically costly, and in practice only species with relatively small eggs lay large clutches with one day intervals between eggs, though with the Anatidae a notable exception in this respect.

Since egg-laying is so sensitive to environmental energy resources the level of the female's energy reserves is a significant determinant of clutch size, not only in precocial species (Ryder 1970, MacInnes et al. 1974) but in altricial species as well (Jones & Ward 1976). Consequently, the situation is particularly open to male assistance in diverse forms e. g., by completely relieving the female of early incubation duties to allow her replenish

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her depleted reserves, as in the Manx Shearwater *Puffinus puffinus*, by guarding the female against interruption of her foraging during the laying period, as in various waterfowl, or by courtship feeding of the female, which in the Great Tit may account for 40% of her requirements (ROYAMA 1966, KREBS 1970). In the case of the Common Tern *Sterna hirundo* the success of the clutch in producing fledglings can be traced back to the extent of courtship feeding of the female by her mate (NISBET 1973).

The incubation period

Several passerine species have been shown to recoup some or all of the fat and protein losses they suffer during egg-laying over the course of the incubation period (JONES & WARD 1976, SCHIFFERLI 1976). In keeping with this the energy expenditure of incubating birds has been found to be up to 25% below the level of a non-incubating individual (WALSBERG & KING 1978, in press), in part because of the more favourable microclimate at the nest-site and in part because of the nest's insulation.

The energetics of incubation when both species share the task has been dealt with by RICKLEFS (1974), but he paid less attention to the single-sex intermittent incubation pattern used by about 31% of bird species (VAN TYNE & BERGER 1966). In a study of this incubation mode WHITE & KINNEY (1974) found that nest attentiveness varied with ambient temperature in inverse hyperbolic fashion, with increase in attentive time at low temperatures being recruited largely from non-foraging time. A sensitivity analysis of these authors' model for intermittent incubation shows that egg temperatures are most susceptable to changes in egg cooling rates, a result in keeping with the general trend towards bulky and well-insulated nests in single-sex incubators and in keeping with a correlation between nest attentiveness and nest conductance observed in nests of the Village Weaverbird *Ploceus cucullatus* (WHITE & KINNEY 1974).

Growth patterns

Nestling and chick growth have received increasing attention from researchers of late, with the resulting emergence of a number of new perspectives. RICKLEFS (1973, 1974) reviewed growth patterns in birds in relation to four hypotheses based respectively on ideas of predation, of energy limitation, of nutrient distribution problems in growing birds, and of precocity constraints. No evidence is available which would lead one to question RICKLEFS' rejection of predation pressures as a determinant of avian growth rates. On the other hand, his computational model of the energy limitation idea – that reduced growth rates may reduce the peak energy needs of each young and allow corresponding increase in brood size – can be challenged in the light of recent results. RICKLEFS assumed constant weight-specific metabolism and constant energy density were typical of growth patterns and showed that with constant mortality through the development period maximum productivity would then be obtained from a succession of broods of one young each. A review of metabolism patterns in nestlings shows metabolic intensity to be most often a power function of nestling weight and this can lead to peak productivity at brood sizes greater than one; the dependence of productivity on metabolism and energy density parameters is too complex to be useful for generalization. RICKLEFS' (1969) model is also open to criticism because the energetics of incubating several eggs at once (rather than a series of one-egg clutches) do not obey his assumptions. Finally, the model fails to take

into account the post-fledging mortality of early broods during the rearing of later ones. An alternative formulation of the brood reduction versus growth rate adjustment dichotomy (O'Connor 1978a) shows that growth rate adjustment can be viable over a restricted range of predation intensities. Dunn (in press) has reached the same conclusion from considerations of ecological constraints on life history tactics. It is thus by no means clear that energy limitation of growth rates should be rejected as an explanation of observed growth patterns.

Ricklefs (1973) recognized the possibility that growth rates were limited by problems of distributing nutrients about the body of the growing bird. Ricklefs discounts the hypothesis on the grounds that there is little variation in growth rates across species with diverse foraging energetics and because gross changes in growth rates do not accompany the changes in diet and selfsuffiency taking place at hatching. Against this I have shown (O'Connor 1977) that several species develop body organs differentially during growth in a manner consistent with a distribution of available nutrients to tissues currently limiting development. The problem with both Ricklefs' and my own arguments here is that each can be turned about in a classical chicken-egg argument. There remains a need for an unequivocal test of this particular hypothesis.

The precocity hypothesis advanced by Ricklefs (1973) suggests that growth rates in birds are limited by the amount of mature function a bird's tissues are called upon to sustain, mature functioning being inconsistent with continued development. This hypothesis has been considerably strengthened by Ricklefs' recent studies (Ricklefs & Weremiuk 1977, Ricklefs in press and in unpublished manuscript): these show that overall growth rates in birds are well-correlated with the proportion of muscle functioning in the young bird at any time, with the rate of muscle growth itself depending markedly on the retention of cellular capacities for DNA uptake and cell proliferation.

Acceptance of either the energy limitation or the precocity hypotheses transfers the emphasis on growth patterns to the ecological constraints requiring particular forms of development. Thus Ar & Yom-Tov (1978) find that precocial development with its correlates of slow growth and foods easily accessible to independent young should be particularly well-suited to Temperate Zone environments; their data in fact confirm a distinct bias towards precocial development outside the tropics.

Several authors have developed an essentially ecological approach to growth pattern studies over the last few years (O'Connor 1979b, 1978c, Bryant 1978, Bryant & Gardiner in press, Ricklefs et al. in press, Dunn in press, Howe in press). Both Dunn (in press) & O'Connor (1978b) have sought to identify broad environmental characteristics which tend to canalize growth patterns into restricted suites of co-adaptations. Thus nestling growth may be constrained by prior clutch adjustment to predictable changes in nestling food supplies, by the need to store fat or otherwise accommodate to unpredictable fluctuations in parental feeding capacities, or by sibling competition (O'Connor 1978b). Werschkul & Jackson (1979) have demonstrated that growth rates are significantly faster in species with clutches of more than one egg than they are in single egg species, a result implying a dominant role for sibling competition. This is supported by my theoretical analysis of brood reduction strategies in birds (O'Connor 1978a) which showed, first, that sibling competition tends to favour brood reduction sooner than does the parent, and secondly, that any risk of predation tends to favour brood reduction.

Egg size and growth

The role of egg size as a determinant of growth has attracted considerable attention following SCHIFFERLI's (1973) paper. SCHIFFERLI showed that large eggs resulted in Great Tits in faster growth and better survival on the part of the chicks. These effects have been traced for several species to the benefits a large egg confers in the face of sibling competition (SCHIFFERLI 1973, PARSONS 1970, NISBET & COHEN 1975, O'CONNOR 1978d), but egg quality per se has also been implicated in the case of the Herring Gull *Larus argentatus* (PARSONS 1975) and of the House Martin *Delichon urbica* (BRYANT 1978). Several studies have focussed on the composition of eggs of different size (RICKLEFS et al. in press, AR & YOM-TOV 1978) or of the chicks hatching from them (ibid., O'CONNOR & OWEN in preparation), and show that the larger egg may allow the chick to hatch with enhanced fat or water reserves or with superior integument (and thus insulation). Calculations show that increased hatching weights achieved through the laying of large eggs are an effective but energetically costly way of reducing the development period. The tactic is thus most likely to be driven, when it occurs, by mortality constraints.

The traditional notion that eggs of precocial species are heavier than those of altricial species has been questioned by RAHN et al. (1974). They found that altough precocial species are in general larger in body size than are altricial species the eggs laid by precocial species females of a standard size are no larger nor no smaller than those of altricial species of the same size. These results notwithstanding, my calculations show that the greater energy loading of precocial eggs (AR & YOM-TOV 1978) results in *relatively* greater energy investment in precocial eggs. But there also exists a quite separate correlation of relative egg weight with the presence of neonatal down in a group, a result potentially explicable in terms of early homeothermy if the female can accumulate feather precursors into the egg more readily than into a chick (O'CONNOR in preparation). This would then explain the greater yolk reserves of precocial chicks (SCHMEKEL 1960) as the fuel for this thermoregulation (AR & YOM-TOV 1978).

The energetics of hatching asynchrony

Hatching asynchrony is the normal prerequisite for brood reduction (LACK 1956, RICKLEFS 1965, O'CONNOR 1978b), but an alternative view is that it allows a reduction of peak brood energy requirements (BRYANT & GARDINER in press, HOWE 1978, ROTH unpublished manuscript). BRYANT & GARDINER found that peak brood requirements were reduced by 8% through asynchronous hatching. Computational studies of my own show that such savings are most significant at high growth rate and in chicks with high energy densities, conditions holding for House Martins. The energy savings are substantially greater with 48 hour rather than 24 hour intervals between eggs hatching. In practice, though, the total energy requirements of most young studied to date appear to plateau (rather than peak) with age, so the scope for energy spreading through asynchrony is restricted.

Nestling metabolism

Nestling metabolism at thermoneutrality is allometrically related to body weight (of the nestlings) in a variety of species (MERTENS 1977a, this study). For precocial species the

regression equations parallel and lie close to the ASCHOFF-POHL equation for non-passerines but for altricial passerines the weight dependance is steeper than for interspecific variation between adults. This rapid increase in metabolic intensity may be related to the relative increase in heat-generating body components such as the pectoral muscles (O'CONNOR 1975a, 1977). Superimposed on these patterns is an increase in the body temperature to which metabolic rate is regulated (O'CONNOR 1975b, MERTENS 1977a). The physiological capacities of a nestling for independent homeothermy are strongly linked to growth rate (DUNN 1975) but the occurrence of endothermy in natural nests is more closely determined by brood metabolism than by individual performance under test (MERTENS 1969, E. H. DUNN 1976). Data in MERTENS (1977b) reveal that for Great Tits brood biomass is more important than plumage insulation or nest insulation, though this last is ecologically variable between species (O'CONNOR 1975c). In large broods nestlings may be at significant risk from hyperthermia (VAN BALEN & CAVE 1970, MERTENS 1977a) and this may set upper limits on the size of clutch which may be safely laid (MERTENS 1977a, KARLSSON & NILSSON 1977).

Discussion

The material reviewed briefly above draws attention to several points. First, we know little of nest insulation properties, yet they influence the energy budget of the breeding pair from the very onset of laying. Second, the energy partitioning possible through the breeding attempt is non-additive, so that expenditure of energy in one part of the cycle can have disproportionate effects on a later stage of the cycle. It may be not without significance that much of the coupling reviewed was between the periods of greatest energy limitation. Finally, if energy is indeed a determinant of growth patterns in birds it probably acts through ecological constraints on sibling competition rather than on a simple energy partitioning model.

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Any attempt to pull together a set of "state of the art" ideas for an overview of current interests in a field depends heavily on seeing other people's manuscripts before publication. I am most grateful to all those who let me see their work ahead of publication.

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Energetics of Avian Moult

James R. King

Avian moult is undoubtedly a period of intensive physiological adjustment in which as much as a quarter of a bird's lean dry body mass is shed and regenerated in the form of feathers (Chilgren, 1977; Gavrilov & Dolnik, 1974; Myrcha & Pinowski, 1970; Newton, 1968). This involves not only a reorganization of the integument for the synthesis of keratin, but also a general intensification of amino acid metabolism (Gavrilov & Dolnik, 1974; Newton, 1968), modifications of water balance (Chilgren, 1975; Gavrilov, 1974), a cyclic osteoporosis correlated with the intensity of moult (Meister, 1951), and an increase of blood volume (Chilgren & deGraw, 1977). The sum of these and other adjustments entrained by moult potentially requires modification of a bird's energy budget, and thereby impinges on other vital functions in the annual cycle. A bird may adjust by (1) increasing its nutrient intake to sustain the additive costs of moult, (2) reducing some other component(s) of the energy budget (e.g., locomotor activity) by a compensatory amount while maintaining stable nutrient income, or (3) utilizing body reserves of energy and protein if exogenous supplies are inadequate. Obviously, any combination of these adjustments might be exploited, but only the third category is a "stress" in the physiological sense, and is apparently rare. The other two may impose ecological "stresses" only by diverting energy or time from other vital functions.

The assumption that moult is a physiological stress has been questioned in passing by King & Farner (1961) and by Payne (1972), but the recognition of reliable generalizations is complicated by the paucity of data and the great variety of avian moult patterns (King, 1974) and nutritional adjustments. This review focuses on energy metabolism and selected aspects of amino acid metabolism during moult. Because of its necessary brevity it is less then comprehensive, and can illuminate only selected conclusions and problems, shorn of supporting detail.

The energy budget during moult

A rigorous approach to the analysis of moult energetics requires the specification of an energy-balance equation, since this reveals immediately the components of energy flow and their interrelations:

$$ME = B + (T_n \pm T_m) + A + P_f + N_f$$

where ME = total daily energy expenditure by a bird in which body mass, composition, and temperature are stable except for material changes resulting from the growth of new plumage; B = basal energy expenditure; T_n = thermostatic energy requirement of nonmoulting birds; T_m = thermostatic increment or decrement resulting from changes of tissue and plumage insulation during moult; A = energy expenditure in somatomotor and autonomic activity above the resting level; P_f = energy required in producing new mass (feathers); and N_f = metabolizable energy increment, if any, of ration required to supply essential amino acids. The last term is difficult to define as a separate component, since the extra energy income potentially contributes also to other terms of the energy budget. The

Department of Zoology, Washington State University, Pullman, WA, USA

term P_f includes the caloric content of new mass plus the energy required in its synthesis. The latter is detectable as a heat increment of synthesis added to the basal power consumption, B.

The energy metabolism of moulting birds has been investigated by measurements of oxygen consumption, metabolizable energy intake, and by estimation of the energy intake required to supply the sulfur-containing amino acids needed in feather synthesis. As will be shown later, the results reported thus far from the use of these methods are surprisingly concordant in view of the improbability that their underlying assumptions (rarely stated) are all fulfilled.

Measurement of oxygen consumption

Measurements of oxygen consumption are typically made at night or during the normal rest period. The growth rate of feathers is apparently uniform throughout the 24-h cycle (NEWTON, 1966) and so nocturnal oxygen consumption under basal conditions will include the heat increment of synthesis. Reports thus far for a variety of species, mostly passerines, all reveal increases of oxygen consumption during moult that range as maxima from about 9% to about 35% above the premoult levels (CHILGREN, 1975; GAVRILOV, 1974; GAVRILOV & DOLNIK, 1974; KOCH & DE BONT, 1944; LUSTICK, 1970; PEREK & SULMAN, 1945). For instance, CHILGREN (1975) showed in *Zonotrichia leucophrys gambelii* caged indoors that oxygen consumption at 25° C was correlated with the intensity of postnuptial moult, changing from a premoult value of 0.469 W to 0.589, 0.620, 0.630, and 0.589 W, respectively, in four successive stages of moult, and stabilizing at 0.445 W in the postmoult period.

The range of variation among these species and studies (9-35% increments above premoult levels) may result from differences in thermal acclimation, the intensity of moult itself (a function of duration, and the mass of plumage regenerated), and body size. If variables (e.g., the sleeping pattern of the experimental birds) other than P_f remain constant throughout the moult period, then these increases of power consumption in the thermoneutral zone reflect the heat increment of feather synthesis. This is the least equivocal (i.e., involves the fewest assumptions) of the methods for estimating this cost, but requires fairly frequent sampling during the course of moult. Only the data of CHILGREN (1975: Table 4) on the postnuptial moult of *Z. l. gambelii* are adequate for this thus far. By assuming that the measured 0_2 consumptions are stable within each of four arbitrary stages of moult, each about 15 days long, it can be estimated that the heat increment of synthesis [P_f $(1-e_p)$, where e_p is the partial or net efficiency of synthesis] in this bird requires 839 kJ. The energy content of the new plumage is equal to the product of its dry weight (1.72 g) and its heat of combustion [21.7 kJ/g (CHILGREN, 1975)], or 37.3 kJ. The total caloric investment in new plumage is thus approximately 839 + 37 = 876 kJ, or 509 kJ/g of new plumage. This resembles estimates from less direct methods (see beyond).

If the insulative quality of the plumage or tissues diminishes during moult, as has generally assumed to be true, then the costs of feather synthesis (P_f) when air temperature is below the lower critical temperature will be augmented by an extra thermostatic costs (T_m). Total or whole-body heat conductance (including evaporative heat transfer) indeed increases in proportion to the intensity of moult (CHILGREN, 1975; GAVRILOV & DOLNIK, 1974: conductances estimated from slopes in Fig. 13), or is at least lower after moult than

before it (POHL, 1971). This does not necessarily mean, however, that the sensible heat transfer (radiation and convection) from the bird's plumage increases during moult, since the interpretation of these data is confounded by a substantial increase in the fraction of total heat lost by evaporation of water during moult. This is associated with an increased turnover of body water, expressed in both increased water consumption (J. D. CHILGREN, pers. comm.) and urinary excretion (GAVRILOV, 1974). When heat transfer by evaporation is subtracted in the computation of whole-body conductance (CHILGREN, 1975; GAVRILOV, 1974: by manipulation of data in Tables 2 and 3) it appears that sensible heat transfer from the integument is unaffected by moult, or is augmented by a statistically insignificant amount (CHILGREN, 1975). It seems safe to conclude from a variety of investigations that total insulation is better (conductance is less) after moult than before it; but the data available thus far do not clearly support the assumtion that integumentary changes during moult cause an increase in sensible heat loss.

Measurements of metabolizable energy intake

Several attempts have been made to estimate the energy costs of moult (P_f, or $P_f \pm T_m + N_f$) by measuring metabolizable energy (ME) consumption by caged birds before, during, and after moulting (BLACKMORE, 1969; CHILGREN, 1975; DAVIS, 1955; GAVRILOV, 1974; GAVRILOV & DOLNIK, 1974; WEST, 1960, 1968) on the basis of the supposition that an increase of ME during moult as compared with a control period before and/or after moult represents the "productive energy" associated with feather synthesis and added thermostatic costs, if any. The accuracy of this method depends heavily on the fulfillment of the rarely stated assumption that energy expenditure in locomotion and associated processes (A, in the balance equation) is the same during control periods and moult periods. It is, however, a well-documented fact that perch-hopping activity in at least some species of birds diminishes by as much as 90% (e.g., EYSTER, 1954) during moult as compared with control periods, mimicking the quiescence of free-living birds, when moulting (for reviews, see CHILGREN, 1975; KING, 1974). Analysis of the allocation of ME to various functions is further complicated by the strong temperature-dependence of locomotor activity in caged birds of several species (KENDEIGH, 1974). In short, the caloric cost of locomotor activity is an uncontrolled and unquantified variable in this experimental system, as already noted by CHILGREN (1975), and reciprocal variation of the terms P_f and A (at least) in the energy-balance equation cannot be detected or evaluated in caloric terms.

Metabolizable energy intake during moult in *Z. l. gambelii* (CHILGREN, 1975), *Passer domesticus* (DAVIS, 1955), and *Lagopus lagopus* (WEST, 1968) caged outdoors did not differ significantly between premoult and moult periods, implying (if the assumptions of this method are accepted) that moult entails no caloric cost or that the cost is so small that it is concealed by statistical error. The measurements of oxygen consumption mentioned earlier, however, show that this is incorrect. CHILGREN's investigation (1975) of ME intake by *Z. l. gambelii* showed that there was a marked decrease of perch-hopping activity that essentially compensated for the reciprocal and concurrent increase of power consumption by moult. A similar compensation is implied by WEST (1968).

In contrast, in several other populations or taxa of *P. domesticus* and *Fringilla coelebs*, ME intake is directly correlated with the intensity of moult (GAVRILOV, 1974; GAVRILOV

& Dolnik, 1974) at all air temperatures investigated. In these investigations, unlike those mentioned above, a concurrent decrease of locomotor activity apparently did not mask, or did not fully mask, the energy costs of moult. The estimates of $P_f + N_f$ for these species agree almost exactly with those of another technique (see beyond), leading to the conclusion that locomotor activity costs in Gavrilov's experiments were invariant through time. This is fortuitous. The discrepancy between these results, however, and those of Chilgren (1975), Davis (1955), and West (1968) makes it clear that the measurement of ME as an estimate of moult costs is not adequate for all species or experimental settings.

Amino acid metabolism in relation to energetics during moult

The amino acid composition of feather keratin differs slightly among species (Harrap & Woods, 1967), but in general the cystine concentration ranges from 6.8 to 8.2 g/100 g of dry keratin (Ward & Lundgren, 1954). Newton (1968) was evidently the first to point out in relation to moult that cystine (major) and cysteine (minor) are much more concentrated in feathers than in the animal proteins (0–6.3 g/100 g) and especially the plant proteins (0–2.9 g/100 g) eaten by birds. Birds during moult might therefore consume food in excess of caloric or other nutritional requirements in order to extract essential amino acids. Moss (1977) suggests that this occurs also in *Lagopus lagopus* during ovogenesis. The term N_f in the energy balance equation symbolizes this excess energy intake.

Taking their cue from Newton's (1968) observations, Gavrilov (1974) and Gavrilov & Dolnik (1974) devised a theoretically ingenious method to estimate the increment of ME (N_f) needed to supply cystine for feather synthesis. This depends on (1) knowledge of the cystine content of feathers and the mass of feathers produced during moult, the product of which is the total cystine requirement, (2) knowledge of the cystine concentration in food, and (3) the caloric density and amount of food eaten. Manipulating these terms (eq. 5.63 in Kendeigh et al., 1977) yields the caloric intake entrained by dietary supplies of cystine incorporated into keratin. Gavrilov (1974) reports that the energy intake associated with feather synthesis (N_f) estimated by this methods matches that in 7 paired measurements by the ME method ($P_f + N_f$) with a mean algebraic error of −0.5%, or 3.3 kJ per moult. If this is so, then N_f must be substituting completely for P_f in the second method, since the two methods theoretically quantify different elements of the energy budget.

The accuracy of the amino acid method in estimating N_f requires the fulfillment of at least two unstated but crucial assumptions. First, it is assumed that cystine (or cysteine) cannot be synthesized from other amino acids; but this is incorrect, since either or both can be synthesized from methionine via homocysteine (Boorman & Lewis, 1971). It is well known that they are only "relatively indispensable" in the diet of birds, and are required only when rates of syntheses involving them exceed the rate at which they can be produced from methionine. Moulting chickens fed a laying ration suffer a negative sulfur balance only when feather replacement is intense (Holman et al., 1945), and the negative nitrogen balance of such chickens when they are fed cystine is reduced disproportionately to the nitrogen content of the added cystine (Ackerson & Blish, 1925), suggesting that exogenous cystine plays a role in keratin synthesis that is otherwise fulfilled by an accelerated turnover of methionine. Studies of amino-acid balance in chickens verify this

(LEVEILLE et al., 1960). The application of this method for estimating N_f would be unquestioned only if a truly essential amino acid (e.g., leucine or threonine, among others) were used as the tracer substance.

A second assumption is that all of the extra ME associated with cystine (or any other amino acid) intake for feather synthesis is allocated to the chemical work of keratin formation and attendant transport processes, and that none of this energy is used in maintenance functions (i.e., that it is completely additive to maintenance requirements). Data with which to test this assumption are scant, but those of LUSTICK (1970), CHILGREN (1975) and GAVRILOV (1974: Fig. 1) are all consistent in showing that power consumption (BMR or ME) in relation to air temperature and/or moult stage is greater at all air temperatures during moult than it is before or after moult. This indicates that the greater heat production during moult does not substitute, or does not substitute fully, for the thermostatic requirement, and is thus additive. This is reminiscent of the addition (or nonsubstitution) of the heat of locomotor activity to the maintenance requirements in certain species and experimental setting (HART, 1971), and is consistent with the view expresses by GAVRILOV & DOLNIK (1974) that the extra heat production during moult is a thermoregulatory burden at moderate to high environmental temperatures, requiring increased evaporative heat transfer.

Conclusions

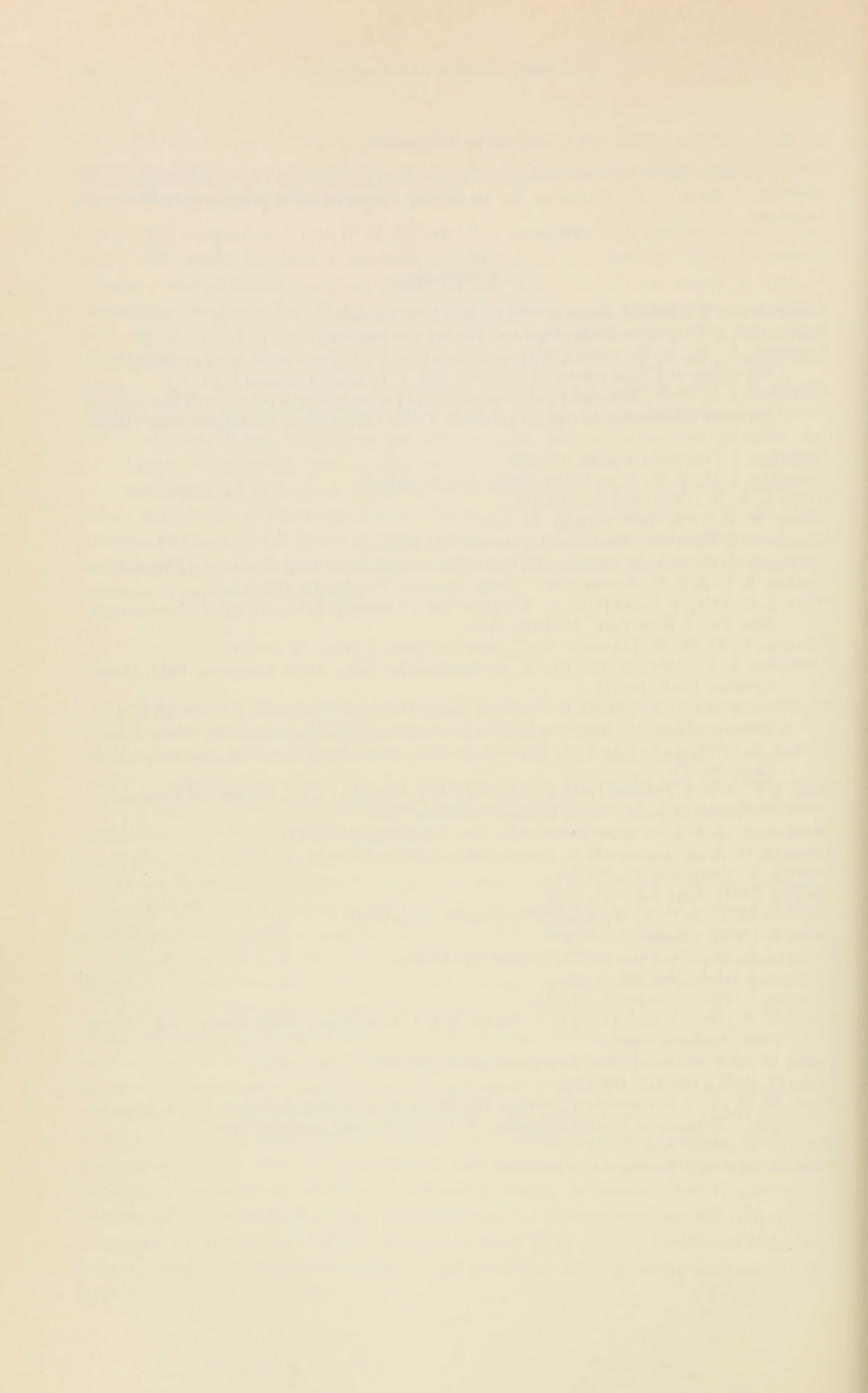
It will be obvious by now that it is not easy to measure accurately the energy costs of moult (or any other productive process) accurately, and that the methods used thus far include many hidden assumptions that may or may not have been fulfilled. It seems, in fact, a remarkable coincidence that the estimates by the ME-intake and the amino-acid methods agree so well (0.5% difference) with each other and with the aforementioned calculations from 0_2 consumption using the data of CHILGREN (1975). Eight studies of various subspecies and age classes of *P. domesticus* and *F. coelebs* reported by GAVRILOV (1974) and KENDEIGH et al. (1977) range from 419 to 510 kJ/g of new feathers produced, averaging (± SD) 464 ± 33.7 kJ/g. The estimate of *Z. l. gambelii* by the O_2 method at 25°C is 509 kJ/g, and the grand average for all 9 cases is 469 ± 34.3 kJ/g. Largely from the same data set, KENDEIGH et al. (1977) computed 448 kJ/g (107 kcal/g), but the difference is trivial. A sparrow producing 1.6 g of new plumage thus consumes about 1.6×449 = 797 kJ in moult. Through a 60-day moult period this averages 13.3 kJ/day, or about 16% of the approximately 84 kJ/day that a caged 25-g sparrow metabolizes at moderate air temperatures. If the partial (net) efficiency of keratin synthesis is 70% (a reasonable value for productive processes) and the heat of combustion of keratin is 21.7 kJ/g (CHILGREN, 1975), then the energy invested in keratin synthesis per se totals only 52.7 kJ and averages 0.88 kJ/day, or only about 7% of the added cost of moult, exclusive of added thermostatic expenditure (if any). This seems to indicate that the costs of moult involve metabolic or nutritional processes in addition to simple synthesis of keratin, but it cannot be emphasized too strongly that these measurements and observations are still subject to a substantial uncertainty, and should not yet be petrified as dogma. Additional investigations are needed, in which the energy budget should be dissected more thoroughly than heretofore.

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SYMPOSIUM ON TEMPERATURE REGULATION IN BIRDS

11. VI. 1978

CONVENER: WERNER RAUTENBERG

Temperature Regulation in Cold Environment

WERNER RAUTENBERG

Introduction

The bird are warm-blooded animals as well as the mammals and adjust their internal body temperature to a constant level of about 38—42° C nearly independently of the level and the fluctuations in ambient temperature. However, many birds live continuously or during their breeding periods in relatively cold biotops. Thus, the gradient between body and air temperatures often reaches thirty and more degrees centigrade. Such environmental cold does cause a variable heat loss from the birds which must be compensated for if body temperature is to be maintained constant. A constant internal temperature of a body results whenever the rate of internal heat production equals the rate of heat loss to the environment. A disturbance in either of these parameters must be countered by adjusting the other if internal temperature is to be regulated. A decrease of the ambient temperature, for example, increases the heat loss of the bird. To prevent hypothermia the animal must reduce its heat loss, and when this action is insufficient to resist the cold stress it must also increase its metabolic heat production. The birds have evolved some effector mechanisms for controlling both their heat loss and their internal heat production.

Control of heat loss

Heat loss to the environment results whenever the ambient temperature is below the body temperature of the birds. The intensity of the heat loss depends on the steepness of the gradient between the body and ambient temperatures, the size of animal and the insulation of the body surface. The heat flow from the body to the environment occurs by radiation, evaporation, conduction and convection. In a cold environment the loss by evaporation is small and can hardly be regulated by the animal. However, the radiation, conductive and convective heat loss can be influenced by changing the blood flow through the skin and the posture of feathers.

Vasomotor responses

A vasoconstriction of the blood arterioles in the skin reduces the heat transport via circulation from the core to the skin and thereby via conduction and radiation from skin to the environment. Countercurrent circulatory systems in the poorly insulated skin areas (EDERSTROM & BRUMLEVE, 1964; GRANT & BLAND, 1930; JOHANSEN & MILLARD, 1973) assist the vasomotor response and minimize the heat efflux from the exposed areas (e. g., unfeathered feet). The vasomotor response is obviously controlled by a temperature regulatory centre which is localized in the anterior hypothalamus (HISSA & RAUTENBERG, 1974; RAUTENBERG & NECKER, 1975; SIMON et al., 1977). The control action of this hypothalamic centre may be stimulated by temperature signals generated in sensors of the skin, the spinal cord and the hypothalamus (HAMMEL et al.,

Ruhr-Universität Bochum, Institut für Tierphysiologie, D-4630 Bochum, Bundesrepublik Deutschland.

1976; Necker, 1972, 1973, 1975; Rautenberg, 1969a, b; Rautenberg et al., 1972, 1978; Rosner, 1977; Simon et al., 1976).

Pilomotor responses

Piloerection of feathers increases the distance between the skin and the outside of the plumage where a calm air layer surrounds the bird through which the heat is transfered by conduction and radiation. Only outside the plumage can the heat be transported away by convection. Since the heat conduction in the air is very small, the fluffing of feathers increases the amount of external insulation by three to fourfold of the value of sleeked feathers (Biebach, 1978; McFarland & Budgell, 1970; Rautenberg, 1967; Veghte & Herreid, 1965). Richards (1977) found that the dry heat transfer in poorly feathered fowls is two times greater than in normally feathered birds at 20—25 °C. Thus, the covering by feathers and their erection is a very important factor for heat conservation in the endothermic birds. The posture of the plumage may be controlled in the same manner as the vasomotor responses (McFarland & Budgell, 1970; Rautenberg, 1969b; Rautenberg et al., 1972).

These two effector mechanism are used by birds during rest and allows them to influence their rate of the heat loss in few seconds. The energetic cost for these responses is very small. The pilo- and vasomotor reactions essentially effect the regulation of the internal body temperature within the neutral temperature zone whose range is specific for the different avian species (Irving, 1964; Scholander et al., 1950).

Behavioral responses

The above described responses can be augmented by species specific thermoregulatory behavior. Many field studies have shown that birds prefer calm, dry and warm places in their biotops during bad weather (Dawson & Hudson, 1970). By this manner of temperature selection, the birds influences its microclimate and thereby its heat loss. But such behavior can only be effective if the environment offers appropriate alternative microclimates. It depends also on other motivations which may dominate temporarily thermoregulatory behavior of the bird (e. g., breeding or feeding). Under laboratory condition where animals are shielded from other things, a trained bird precisely selects its prefered temperature and thereby regulated its body temperature with minor contributions from the other thermoregulatory effectors (Budgell, 1971; Laudenslager & Hammel, 1977; Schmidt, 1978; Schmidt & Rautenberg, 1975). This conditioned thermoregulatory behavior may indicate the capacity of the behavioral temperature regulation. It seems to be preferentially controlled by temperature signals generated in the skin. But information from changes in core temperature are also evaluated (Schmidt, 1976).

Acclimatisation

The heat loss to the environment is also influenced by acclimating processes which alter the insulation of the surface by a deposition of subcutaneous fat and by the thickness of plumage after the moult. These processes require a long time and go along with the annual cycle. They appear to be controlled by the endocrine system (Chaffe & Roberts, 1971; Dawson & Hudson, 1970). They shift generally the thermoneutral

range to lower ambient temperatures and effect cold acclimatisation of the metabolic processes in the exposed areas (e. g., in the function of foot nerves in arctic birds, IRVING & KROG, 1955). Acclimatisation increases whole body insulation of birds, but hardly influences the effectiveness of pilo- and motor responses.

Control of heat production

All the thermoregulatory mechanisms described above serve to reduce the heat loss of birds in a cold environment. They require a small energetic cost and stabilize the internal body temperature in a resting birds within a distinct range of ambient temperature. When the ambient temperature decreases below this range, the heat loss exceeds the heat production during rest and the bird must increase its rate of the metabolism. A heat gain generally follows from any forms of muscle activity (e. g., tonus of the skeletal muscles, increase of heart rate or action of the digestive organs) or by increasing the cell metabolism (e. g., in liver, kidney or spleen). Although these metabolic processes effects an internal heat gain, they take an uncontrolled course with respect to the equilibration of the heat balance in animals. A controlled heat production in birds is the cold tremor or the shivering of the skeletal muscles.

Shivering

Shivering is a tremor of the skeletal muscles by which heat is produced but no coordinated movements (HEMINGWAY, 1963). The heat gain due to maximal shivering reaches four to five times basal metabolism. This enables pigeons for example to stabilize their internal temperature at an ambient temperature of —70° C (HART, 1962). This thermoregulatory effector mechanism is the most important basis of endothermy in birds and mammals. Shivering thermogenesis has been investigated intensively. Fig. 1 shows that shivering starts in warm adapted and resting pigeons at an ambient temperature of about 20 °C. The cold tremor is forced and the heat production increases with decreasing ambient temperature, thereby the core temperature is maintained at a constant level, whereas the mean skin temperature shows a linear fall. This decrease of skin temperature may be the information used by the temperature control system to activate proportionally the intensity of shivering. There are thermoreceptors in the skin of birds (GREGORY, 1973; KITCHELL *et. al.*, 1959; LEITNER & ROUMY, 1974; NECKER, 1972, 1973) and NECKER (1977) has shown that such receptors at the outside of wings, at the back and the head play an important role for the control of shivering. However the temperature of the body surface is not the only information for the control centre. After cutting the dorsal roots pigeons were able to shiver and to increase their heat production in cold environment as well as intact birds, although the peripheral input was interrupted (NECKER & RAUTENBERG, 1975). The deafferented birds regulated their core temperature at a lower level. Internal temperature sensors obviously mediated the shivering thermogenesis. RAUTENBERG (1967, 1971) and NECKER (1975) demonstrated the high thermosensitivity of the spinal cord in birds. There is additive input from spinal cord and skin temperatures in the control of shivering thermogenesis.

Why does the thermoregulatory system need two or more thermosensitive areas? We have learned before that vasomotor responses and countercurrent systems actively decrease the skin temperature in a cold environment. Many skin areas are so well insu-

lated that they are hardly effected by cold. In other words, the temperature information coming from the skin is irregular and cannot exactly control thermogenesis. Therefore, temperature sensors of the controlled variable (that may be the core temperature) must also inform the regulatory centre of the level of the internal temperature. The interaction of peripheral and central thermodetectors is necessary, because the thermogenesis is proportionally controlled. That means that the driving of the effector action is proportionally correlated with the deviation of the controlled variable as we found in the deafferented birds. But this would always require a decrease of the core temperature to stimulate thermogenesis. However, the birds have solved the problem by developing a peripheral temperature sensitivity which provide feed forward control of the metabolic effector system.

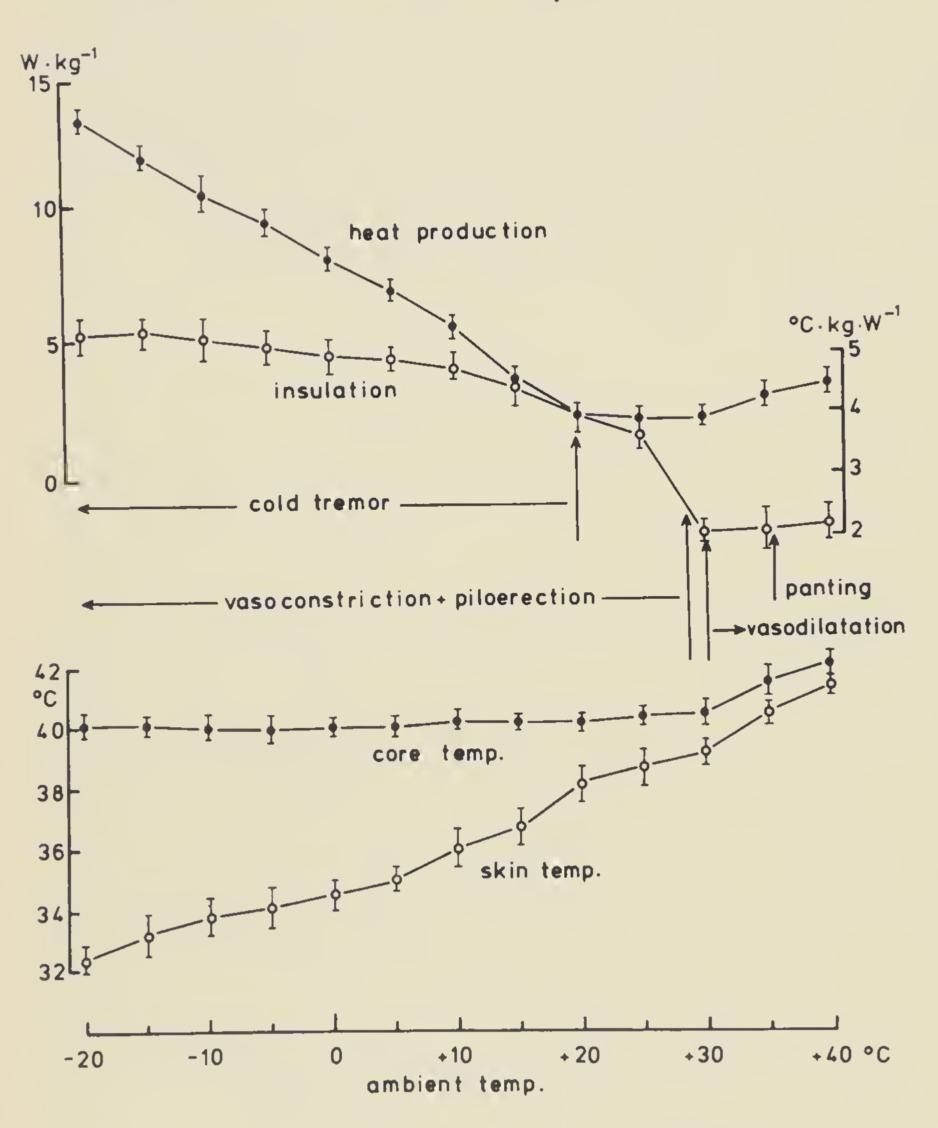


FIGURE 1. Thermoregulatory responses and body temperature in relation to ambient temperature in pigeons.

Conclusion

Thermogenetic shivering makes the birds independent of the environmental temperature. But the effectiveness of shivering is dependent upon the amount of external insulation by feathers. Poorly feathered fowls are unable to maintain a constant core temperature below 10° C ambient temperature, although they increased their rate of heat production to double that of normally feathered birds (RICHARDS, 1977). Likewise shivering and the full capacity of temperature regulation is developed in young birds together with the growth of their feathers (MCNABB & MCNABB, 1977). Thus, the temperature regulation of birds in cold environments is based primarily on the developing of feather insulation and shivering thermogenesis.

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Physiology of Heat Dissipation

S. A. Richards

Introduction

The greater part of the energy derived from the breakdown of food is used by the endothermic animal in maintaining a constant body temperature. The rate of metabolic heat production is varied according to the prevailing thermal conditions in the external environment, and the stability of the internal temperature is achieved by balancing this side of the heat flow equation with the opposing side, that of the rate of heat loss. It is the purpose of this brief article to provide an illustrative, not a complete, summary of this latter aspect, with emphasis on the responses of birds to heat exposure, using examples selected mainly from material published since the more comprehensive reviews of Calder & King (1974) and Whittow (1976).

Non-evaporative heat exchange

Basic physical mechanisms

Heat produced in the body core is lost to the environment through the general body surface and the surface of the respiratory tract. It is transported to the surface directly by conduction through the tissues of the body shell and indirectly by convection in the blood stream. Sensible transfer to the environment then occurs by conduction, convection and radiation through and from the insulative barrier represented by the boundary layer of air trapped in the plumage. Conductive loss to the air is minimal because of the low thermal conductivity of this medium, although compression of the plumage during diving leads to a significant increase by reducing the thickness of the insulating boundary layer (Kooyman et al., 1976). Conduction to water form the legs and feet is rapid when there is an adequate thermal gradient: in cold conditions this is minimized by counter-current heat exchange, but it becomes substantial when peripheral blood flow must be increased to prevent freezing of the tissues (Kilgore & Schmidt-Nielsen, 1975). Convective transfer can account for a large proportion of total sensible heat loss when there is rapid air movement, as for example in flight (see below), while radiant heat exchange is always complex, notably in hot conditions when there may be substantial absorption of heat from the sun. Although for long wavelengths all animal surfaces behave much as perfect black bodies, regardless of colour, significantly more of the energy of the visible spectrum is reflected by light coloured plumage than by dark (Heppner, 1970).

Autonomic influences

The driving force for sensible heat transfer is the prevailing temperature of the body surface relative to that of the core and of the environment. It is by altering this relationship that control of the rate of heat loss is achieved. Such control is exercised by the

Co-author: P. E. T. Hooper

Author's Address: Wye College, University of London, Ashford, Kent. U. K.

activity of the muscles that influence the diameter of the skin blood vessels and the posture of the feathers. However, the significance of these responses is greatest under cold conditions when the task is to conserve heat rather than to dissipate it.

Changes in the blood flow to the feathered skin do, in fact, appear to be minimal, but the unfeathered extremities play an important part in the control of heat loss. In the fowl, for instance, a progressive rise in ambient temperature elicits an abrupt and maximal vasodilatation in the comb and legs at about 27° C (RICHARDS, 1971). However, at the upper limit of the thermoneutral zone there is no more scope for autonomic intervention in sensible transfer and it is at this stage that other responses assume a greater importance.

Behavioural influences

Under stressful climatic conditions the role of behaviour is of paramount importance. Both in nature and in the laboratory behavioural responses often seem to be activated preferentially. By changing the pattern of sensible heat exchange with the immediate environment, they postpone or obviate resort to the more costly metabolic or evaporative mechanisms which, in any case, quickly become dependent upon supplies of food and water.

Whereas autonomic responses are associated with the function of particular organs or systems. behavioural reactions typically involve the whole body and include changes that vary the ratio of surface area to mass, such as the retraction of extremities, and an elaborate variety of manoeuvres that effect changes in the environment itself. These range from long distance migration in search of warmer or cooler climates to the use of windbreaks, burrows and crevices, as well as huddling together and nest building. There is good evidence that such responses have biological value. For example, the survival of Willow Grouse *(Lagopus lagopus)* chicks depends upon basic thermotropic activity and the shortening of foraging periods in bad weather (MYHRE et al., 1975; BOGGS et al., 1977), while huddling between domestic fowl chicks permits the maintenance of a higher body temperature at a lower metabolic rate (MISSON, 1976). In the case of the Jackass Penguin *Spheniscus demersus* the problem is one of heat stress on land in a bird adapted principally for survival in cold water. Again the answer is in terms of appropriate behaviour, including the restriction of periods of activity to dawn and dusk, orientation away from the sun, and nesting in burrows (FROST et al., 1976).

In recent years there have been major advances in two aspects of behaviour, those concerning the quantitative analysis of the concept of thermal comfort using instrumental conditioning, and the direct measurement of thermoregulatory parameters in flight. With mammals, the majority of investigations using operant techniques have been concerned with the acquisition of heat-reinforcement behavior during exposure to cold. The first work with birds was also of this type and their ability to work for heat has been demonstrated (although only after 24 to 37 days of training) in the Barbary Dove *Streptopelia risoria* (BUDGELL, 1971), the young Japanese Quail *Coturnix coturnix japonica* (SPIERS, et al., 1974), and the plucked adult domestic fowl (N. R. SCOTT, pers. comm.). However, the experiments of SCHMIDT & RAUTENBERG (1975) with the pigeon and RICHARDS (1976a) und HOOPER (unpublished) with the fowl, indicate that normally feathered adult birds are reluctant to abandon their highly effective postural and insu-

lative defences for thermal reward. In contrast to this, the relatively limited capacity of the birds to tolerate heat showed itself in their readiness to work for reinforcements of cool air in preference to thermal panting. More recently, LAUDENSLAGER & HEMMEL (1977) have demonstrated the capacity of the Chukar Partridge *Alectoris chukar* to learn a response that minimizes thermal stress of either type; the work rate of the birds was related directly to the deviation of the exposure temperature from a preferred range of 25—32° C.

Studies of heat dissipation in flight have progressed rapidly with the development of the necessary wind-tunnel technology. Flight itself has sometimes been seen as a means of increasing convective cooling in hot conditions (MARDER, 1973), but most interest has centred on the question of how the excess heat that is generated by an enormous rise in metabolic rate is actually dissipated. At temperatures up to about 30° C, at least 80 % of the body heat appears to be lost by non-evaporative means to the moving air (although the contribution of cutaneous evaporation has yet to be quantified) (BERNSTEIN, 1976). There is an unavoidable increase in heat flow in unfeathered and poorly feathered areas, notably the feet (BAUDINETTE et al., 1976). Contrary to the earlier view however, the insulation of the plumage over much of the body is increased during flight as a result of feather adjustments. The purpose of this is apparently to limit the rate of heat loss to a level that ensures a sustained hyperthermia of as much as 2—4° C (TORRE-BUENO, 1976), a situation that is likely to increase the efficiency of the flight muscles.

Evaporative heat loss

Under very hot conditions, when sensible forms of heat dissipation and behavioural heat-avoidance are no longer adequate, almost all birds resort to panting in order to maintain thermal homeostasis. Evaporative heat loss is governed by different physical laws from those controlling sensible loss, and depends in essence upon the vapour pressure gradient between the evaporating surfaces and the environmental air and on the resistance to the movement of vapour down the gradient. Evaporation can occur into an atmosphere that is already saturated with water vapour, provided, as is generally the case, that the temperature of the air is below that of the evaporating surface. The body heat that is lost during evaporation is that required to change the state of the water from liquid to gas.

Although birds do not actively secrete water from the skin, a significant proportion of the total water evaporated is cutaneous in origin, as first described by BERNSTEIN (1969) and SMITH & SUTHERS (1969). This appears to be the result purely of a passive process of diffusion that is not under physiological control, and in the fowl, for example, the rate may be expressed as a linear function of ambient temperature (RICHARDS, 1976b). Cutaneous water loss in this species is, in fact, greater than respiratory water loss at all temperatures below about 21° C, accounting for 78 % of the total at 0° C and still for as much as 25 % at 40° C when panting is maximal.

In contrast to the cutaneous water loss, evaporation from the respiratory tract is under close nervous control. Since the surface area for evaporation is essentially fixed, the increase in evaporation that occurs in hot climates is brought about mainly by raising the rate of ventilation of the surface by an enhanced total respiratory volume. In many species the increase commences before the onset of overt panting, but when fully

established, the latter is characterized by a rapid respiratory frequency that more than compensates for the reduced tidal volume.

The most important work on the efficiency of panting has been performed since the demonstration by Lasiewski et al. (1966) that estimates of thermolytic capacity are highly dependent upon the rate of air flow (and hence the humidity) in the metabolic chamber. The outcome of this is that the great majority of birds examined have been shown capable, often for several hours, of dissipating by evaporation a quantity of heat well in excess of metabolic heat production at ambient temperatures between 40 and 45 °C. In a recent study, for instance, the figure for the Budgerigar *Melopsittacus undulatus* was 156 % of metabolic heat at 45° C (Weathers & Schoenbaechler, 1976a). There are exceptions to this however, even among wild tropical birds, such as the Sooty Tern *Sterna fuscata* which relies more upon behaviour (MacMillan et al., 1977), and in our studies of the fowl (acclimated at about 22° C) we have found few individuals capable of withstanding even 40° C at low humidity for much more than one hour.

As to the site of the respiratory evaporation in birds, there has been speculation for more than a hundred years (see Salt, 1964) on the supposed role of the air sacs as additional surfaces for evaporative cooling. Menuam & Richards (1975) however could find no evidence to support this idea. Their results showed that the panting fowl evaporates water from the nasal, buccal and upper tracheal surfaces in much the same way as mammals. Indeed, all recent evidence on the direction of air flow in the avian respiratory system, dating from Bretz & Schmidt-Nielsen (1970), indicates that these surfaces are the only ones that could be ventilated with air not already fully saturated at body temperature.

Many birds vibrate the floor of the buccal cavity ('gular flutter') during heat stress as an additional means of ventilating the evaporating surfaces. This may or may not be synchronised with the panting rhythm, but in either case is undoubtedly of thermoregulatory significance. In the Japanese Quail, for example, elimination of gular flutter reduces the rate of evaporative water loss by about 20 % (Weathers & Schoenbaechler, 1976b). An analagous process, lingual flutter, appears, to operate in some Psittacidae (Weathers & Caccamise, 1975; Weathers & Schoenbaechler, 1976a).

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Diurnal Cycles of Thermoregulation and Hypothermia

RUDOLF GRAF

Introduction

Day-night rhythms of body temperature in birds have been well known for many years (CHOSSAT, 1843). It has been shown that in birds as well as in mammals these temperature rhythms persist, when rhythmical fluctuations of external factors such as light (Zeitgeber) are lacking (ASCHOFF, 1970). The multifaceted problems of endogeneous circadian rhythms will not be discussed here. This paper deals first with the question of how the rhythm of body temperature is generated by the effector mechanisms of heat loss and/or heat production, and whether there is an active adjustment of body temperature on a day-night basis by the thermoregulatory system. Second, the influence of different internal and external factors on the form of day-night temperature rhythms will be discussed. And third, we will consider, whether the different forms of hypothermia and torpor have a similar functional basis as the normal day-night rhythms of body temperature.

Day-night changes of body temperature

In day-active birds, the daily cycles of body temperature normally have a maximum during the day and a minimum during the night (for lit. see DAWSON & HUDSON, 1970); in night-active animals inverse T_b-rhythms exist (SIMPSON & GALBRAITH, 1905/06). Besides this, the form of the temperature cycles is dependent on a variety of factors, e. g., it depends on external conditions such as photoperiod. VEGHTE (1964) showed, for example, that the Gray Jay has an elongated temperature maximum during summer, when the light phase was prolonged. It is remarkable, that under these conditions the rise and fall of T_b in the morning and the evening happen much quicker than in winter.

The range of daily temperature oscillation varies with species. As can be concluded from data of KING & FARNER (1961), the day-night difference of T_b becomes smaller with increasing body weight; a hummingbird, e. g., which is not in a torpid state, shows a range of 8° C (LASIEWSKI, 1964), whereas in the Ostrich there is a range of only about 1° C (CRAWFORD & SCHMIDT-NIELSEN, 1967). Additionally, the birds which become hypothermic or torpid, mostly are small birds with a weight of less than 100 g, as Apodiformes and Caprimulgiformes (DAWSON & HUDSON, 1970). The Turkey Vulture, however, which weighs more than 2000 g, undergoes moderate hypothermia, too (HEATH, 1962). And on the other hand, in most birds with a weight between 30 and 500 g the day-night difference of T_b looks very similar (about 1—3° C) or is dependent on other parameters.

The amplitude of T_b-rhythm is influenced by ambient temperatures.

In warm environments it becomes smaller (DAWSON, 1954; TROST, 1972); both day and night mean values are on a higher level. Exceptionally in the fowl above 35° C T_a

Ruhr-Universität Bochum, Institut für Tierphysiologie, D-4630 Bochum, Bundesrepublik Deutschland

even higher T_b-values were regarded during the night than during the day (VAN KAMPEN, 1974). In neutral and cold environments body temperature levels at day and night and the difference between them become more stable. During the night, there is an increasing fall of T_b with decreasing T_a enlarging the range of daily T_b-oscillation at low ambient temperatures. As we found in the pigeon, during the day even a slight negative correlation can be regarded, so that in low T_a body temperature is higher than in thermoneutrality. The latter phenomenon surely depends on the activity of the bird and therefore on the site of temperature measurement. Within the breast msucle, where most of shivering heat production occurs, and in the vertebral canal the negative correlation is much clearer than in the rectum.

CHOSSAT (1843) showed that day-night T_b-difference is enlarged in starved pigeon, and the same has been fôund in other species (PEIPONEN, 1970; BIEBACH, 1977). Though night temperatures get lower and lower during consecutive days, surprisingly the day temperatures reach nearly the same level. Since on consecutive days distinct levels of T_b are reached (BIEBACH, 1977), it seems that starvation (or the energy content of the body) as well as T_a have some influence on the regulated level of T_b during the night. Even in torpor, which has been considered qualitatively different from homeothermy (CALDER & KING, 1974), T_b appears to be regulated at distinct levels. Poorwills are able to arouse spontaneously from a body temperature of 5° C (LIGON, 1970). WOLF & HAINSWORTH (1972) showed that in several species of hummingbirds rather low T_b-thresholds for metabolic heat production exist during torpor so that T_b is regulated at about 15° C. The influence of nutrition and temperature adaptation both on the entrance into torpor (LASIEWSKI, 1963; BARTHOLOMEW & TROST, 1970; PEIPONEN, 1966) and normal night decrease of body temperature illustrates the similarities between normal T_b-rhythms and daily hypothermic states. Even though a clear distinction has been made between nocturnal torpor and hypothermia with respect to changes in respiration or in muscle coordination (CALDER & KING, 1974), this does not necessarily imply a qualitative difference in thermoregulation. Such a conclusion also can not be drawn from experiments which show that the fall of T_b during the entrance of torpor is similar to a Newtonian cooling curve (LASIEWSKI & LASIEWSKI, 1967). T_b-levels falling near on Newtonian curve reveal only a good adaptation for energy conservation. Whether or not this is a regulated decline in T_b can only be answered by investigation of the controlling system.

Day-night changes of thermoregulatory functions

So far not much is known about the generation of the different body temperature rhythms described above.

Though the T_b-rhythms normally are accompanied by rhythmical changes of locomotor activity, wakefulness and food intake, they are at least partly independent of these variables. For example independence from a rhythm of food intake is evidenced by the fact that day-night T_b-cycles are increased in amplitude during starvation. Metabolism rhythms are as well known in birds as T_b-rhythms, and also seem to be independent from activity as ASCHOFF & POHL (1970) have shown in resting and starving bramblings. The interdependence between body temperature and metabolism cycles is unknown; probably there exists a very close coupling. It is certain, however, that

metabolism and shivering are very strongly correlated, for in birds shivering is the only effector mechanism for extra heat production. It was described by LASIEWSKI et al. (1967), that the Giant Hummingbird reduces electromyographic activity entering torpor. Similarly shivering is reduced in the Poorwill (BARTHOLOMEW et al., 1962) and in the Turkey Vulture becoming hypothermic (HEATH, 1962). During arousal from torpor or hypothermia the birds increase shivering. On the other hand, in the Smooth-billed Ani, shivering seems to play a less important role (WARREN, 1960). As we found in the pigeon for generating normal T_b-rhythm shivering is essential especially in low T_a. For investigation of shivering the EMG of the breast muscle was measured and integrated; at constant ambient temperatures below the thermoneutral zone shivering was reduced shortly after lights-off (LD-conditions of 12:12 hours), and increased again some hours before lights-on. The lower the T_a, the smaller was the reduction of shivering. Additionally under these conditions shivering increased earlier before lights-on, so that the shivering rhythm is both a function of time of day and T_a.

Additionally, we investigated the interdependence of shivering and thermoregulatory behavior in day-night rhythms (SCHMIDT et al., 1977). In an instrumental situation pigeons were given the possibilities to select between a cold and a warm air stream. During the phase of daily decreasing T_b the birds showed a maximum of behavioral heat gain, while during the phase of increasing T_b they showed a minimum, thus enlarging the reduction of shivering during night phase. It must be kept in mind, that this study of thermoregulatory behavior does not imply any conclusion about natural diurnal thermoregulatory behavior.

Nothing is known about the involvement of effectors other than shivering in generating daily hypothermia. In contrast to mammals, where a torpor-decrease of T_b is accompanied by vasodilatation (CHEW et al., 1967), MCMILLAN & TROST (1967) suggest that in birds only a reduction of thermogenesis is responsible for the decrease of body temperature during night. However, in generating normal T_b-rhythms in birds, more effectors are involved. Measurements of conductance show that a day-night change of heat loss exists (TROST, 1972; ASCHOFF et al., 1974). Decreases of heart rate and breathing rate during the night were seen in the fowl at relatively low ambient temperatures (SCOTT & VAN TIENHOVEN, 1971; OSHIMA et al., 1974). In pigeons, we studied the diurnal changes of vasomotor activity and panting at different ambient temperatures for 24 hour periods. Within thermoneutrality we recorded an increase in foot temperature due to vasodilatation during the decrease of T_b. Later on, foot temperature decreased again (vasoconstriction). Feet remained vasoconstricted even in the late dark phase, when T_b was already increasing. At higher ambient temperatures (above thermoneutrality) vasodilatation persisted over 24 hours, but respiratory rate increased significantly shortly after lights-off.

Further experiments demonstrated that reactions elicited by peripheral and spinal short-term stimuli showed similar day-night differences as the investigations of the effector mechanisms. In the day a decrease of T_a was followed by an immediate increase of shivering and heat production, whereas in the night the reaction got smaller and was delayed. The effect of local spinal cooling, too, was much smaller in the dark phase; we measured a downward shift of threshold temperatures for shivering and heat production of about 3° C. In addition, it could be shown, that the daily cycle of spinal thermosensitivity depends upon ambient temperature. The higher the T_a, the lower

were the reactions to the same cold stimuli. On the other hand, the effect of local spinal warming on evaporative heat loss was found to be greater during the night. Thus, the thresholds for both central and peripheral thermosensitivity change during the night in the pigeon (GRAF, 1977).

Conclusion

Regarding the different daily T_b-rhythmus, we can conclude, that the normal range of oscillation is generated at least in the pigeon by a diurnal change of all investigated thermoregulatory functions, with an additional dependence on ambient temperature. This is in agreement with the hypothesis of an active adjustment of the day-night rhythm of body temperature. Especially the increase of breathing rate and thermoregulatory behavior during the daily fall of T_b demonstrate active thermoregulation. A lowered T_b during the inactive portion of the day results in a substantial saving of energy. This is even more true for daily T_b-rhythms with larger ranges (hypothermia and torpor). These rhythms seem to have a similar functional basis as those with normal ranges, which becomes evident from the stabilization of low body temperatures during the night and the involvement of shivering into the generation of these rhythms. Nevertheless more investigations of thermoregulatory functions must be made to test this supposition. After that, the different concepts of hypothermia, torpor and day-night rhythm of body temperature should be reconsidered.

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The Controlling System for Temperature Regulation

H. T. Hammel

The regulation of body temperature in vertebrates is achieved by neural pathways which link receptors with motor responses in order to limit the deviation of core temperature, T_c, from an optimal temperature, T_o, for most body functions. Since the thermal environment may force T_c to exceed T_o or T_c to be less than T_o, most species have evolved a "warm" neural pathway to limit the increase of T_c over T_o and a "cool" neural pathway to limit the decrease in T_c below T_o, as illustrated in Fig. 1. This concept has been derived from the analysis of temperature regulation in mammals (Hammel, 1972). We are concerned here with the controlling system in birds, the portion of the neural elements represented to the left of the double broken line in Fig. 1. We need only note at this time that the controlled system consists of many complex autonomic and behavioral responses activated by the controlling system. In order to caricature the neural network which is responsible for thermal homeostasis in birds, there are many characteristics of the controlling system to be explored experimentally. We shall review some of these and refer the reader to others described by Rautenberg, by Richards and by Graf in this Symposium.

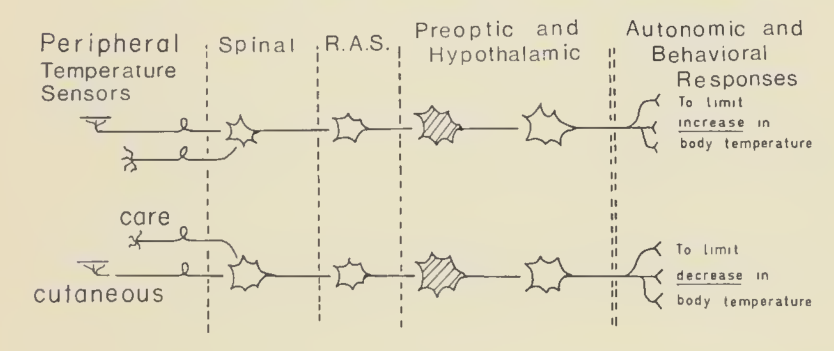


Figure 1. Neural pathways for regulating core temperature. Upper: "warm" neural pathway. Lower: "cold" neural pathway. R. A. S. indicate the reticular activating system.

Deep body thermosensitivity

Brainstem

There are neurons in the hypothalamus of the conscious Peking Duck which increased firing rate as their temperature was increased from 32 to 42 °C (Simon et al., 1977). Some of these neurons increased their firing rate exponentially with a Q_{10} ranging between 2 and 17. In a total of 29 neurons tested for temperature sensitivity, 11 were warm sensitive with an average $Q_{10} = 4.8 \pm 4.3$, 5 were cold sensitive, 5 were insensitive to temperature change, and 8 responded variably to temperature and could not be classified. This assortment of thermal sensitive and insensitive neurons in the hypothalamus of the duck was essentially the same as that recorded in the cat (Eisenman & Jackson, 1967; Nakayama et al., 1963), rabbit (Hellon, 1967), dog (Cunningham et al., 1967; Hardy et al., 1964) and even in a lizard (Cabanac et al., 1967).

Co-authors: E. Simon and Ch. Simon-Oppermann

Author's address: Physiological Research Laboratory, Scripps Institution of Oceanography UCSD, CA 92 093, U.S.A.

As in mammals, there are hypothalamic neurons in the pigeon which increase activity when cooling the spinal cord and/or the skin and there are neurons which increase their activity when heating the skin and/or the spinal cord (ROSNER, G., 1977). From this comparison, we might anticipate that warming and cooling the rostral brainstem of birds would strongly elicit the appropriate thermoregulatory responses observed in mammals. In fact, we shall find that birds are weakly responsive or even respond paradoxically to altering their brain temperature.

Hypothalamic heating:

In some instances warming the hypothalamic tissue elicits the appropriate responses in birds as in mammals. For example, increasing the hypothalamic temperature from a normal temperature of 39 °C to 41 °C in a conscious Adelie Penguin resting in a thermal neutral ambient temperature of 10 °C induced vasodilatation in vessels of the wing as indicated by an increase in wing temperature (SIMON et al., 1976). Associated with this shift of core heat to the peripheral tissue was a slight reduction in esophogeal temperature. But then in the same experiment strong hypothalamic cooling paradoxically reduced vasoconstriction causing an increase in wing temperature. In experiments on the Pekin Duck, warming hypothalamic tissue appropriately increased the rate of evaporative heat loss in a 33 °C environment (SIMON-OPPERMANN et al., in press). In the same experiment when the duck was already panting, cooling the hypothalamic tissue only momentarily reduced panting; the hypothalamic cooling then paradoxically enhanced panting for many minutes which was time enough to lower the core temperature by more than 1 °C and lessen the panting and the rate of evaporative water loss.

The pigeon also rarely panted in response to heating the brain to 44 °C (RAUTENBERG et al., 1972). In an experiment on the pigeon, hypothalamic cooling paradoxically increased the respiration rate for a short time and by an amount depending on the prestimulus panting rate (SCHMIDT, 1976). In one instance in the same experiment, warming the hypothalamic tissue paradoxically inhibited the respiration rate. A pigeon, in a hot environment and trained to interrupt a light beam which caused a burst of cold air to blow over the bird, responded appropriately for more cold air when its hypothalamic tissue was heated and called for less cold air when its hypothalamus was cooled (SCHMIDT, 1976 b). Thus, hypothalamic heating in pigeons may appropriately elicit responses to diminish core temperature. However, paradoxical responses may also be elicited by hypothalamic warming.

Hypothalamic cooling:

Cooling the preoptic tissue of the house sparrow in an ambient temperature of about 25 °C increased $\dot{V}_{O_2}$ by 9 percent while heating the same tissue decreased $\dot{V}_{O_2}$ by 28 percent (MILLS & HEATH, 1972 a). These are small and appropriate effects. On the other hand, cooling the ventral hypothalamus under the same conditions paradoxically decreased $\dot{V}_{O_2}$ by 18 percent.

Cooling hypothalamic tissue in the Peking Duck paradoxically reduced vasoconstriction in the foot web when the vessels were already vasoconstricted and it inhibited shivering when the duck was already shivering (SIMON-OPPERMANN et al., in press). Similarly in an Adelie Penguin that was already shivering at −19 °C, cooling its hypothalamus inhibited shivering, Fig. 2 (SIMON et al., 1976). Furthermore, during the inhi-

bition of shivering, the esophogeal temperature fell by about 1 °C. When the hypothalamic cooling ceased and the tissue returned to core temperature there was a large transient increase in shivering and $\dot{V}_{O_2}$. Little or no effect on $\dot{V}_{O_2}$ was caused by cooling the brainstem of the pigeon (RAUTENBERG et al., 1972) or the California Quail (SNAPP et al., 1977).

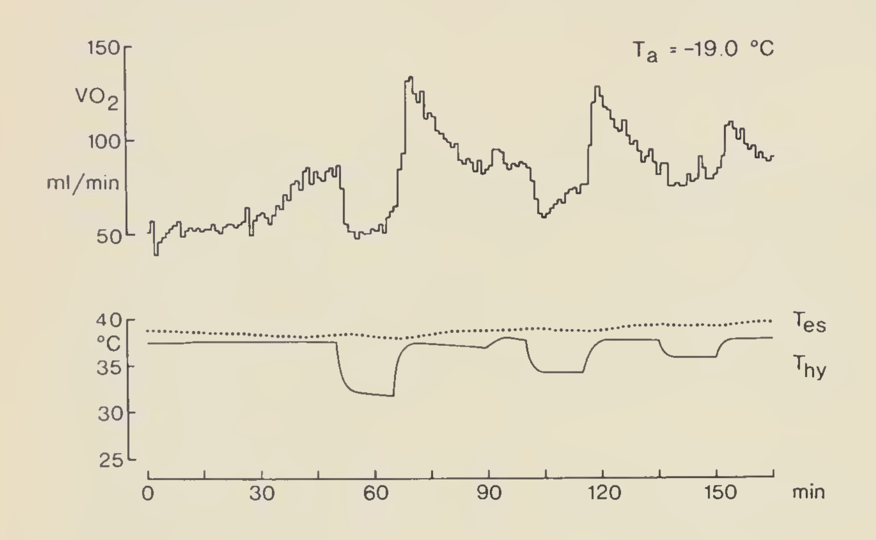


FIGURE 2. Oxygen consumption and core temperature at cold ambient conditions as influenced by cooling of the rostral brain stem. Body weight of Adelie Penguin 4.23 kg. es = esophagus, hy = hypothalamus.

Spinal Cord

Neurons in the spinal cord of the pigeon have been shown to have temperature sensitivity, increasing firing rate with increasing temperature (NECKER, 1975). Furthermore, altering the spinal cord temperature appropriately effects thermoregulatory responses in the pigeon (RAUTENBERG et al., 1972; SCHMIDT, 1976 a), in the Adelie Penguin (HAMMEL et al., 1976) and also in the Peking Duck. Cooling the spinal cord in a cold exposed (T_a = —20 °C) shivering penguin enhanced shivering but did not initiate shivering at warm ambient conditions (T_a = +10 °C). Warming the spinal cord at cold ambient conditions inhibited shivering and induced or increased vasodilatation in a warm environment (HAMMEL et al., 1976). The shivering response to spinal cord cooling was much greater in the pigeon than in the penguin. Perhaps this difference in sensitivity may be attributed to differences in size as is apparently the situation in mammals in which both the spinal cord sensitivity and the hypothalamic sensitivity are inversely related to size.

Peripheral core receptors

Indirect evidence indicates that hypothalamic and spinal temperatures sensitivities cannot explain the entire deep body thermoreceptivity in birds and, thus, suggests the importance of deep body thermoreceptors outside of the central nervous system. Decreasing the core temperature by only 3 °C caused a four-fold increase in the $\dot{V}_{O_2}$ in the penguin (HAMMEL et al., 1977), whereas a similar decrease in spinal temperature may be only slightly stimulating and cooling the hypothalamus would have the obverse effect. The importance of core receptors outside the central nervous system (CNS) calls for more careful investigations to ascertain their sensitivity and location.

Neural Network

In birds, as in mammals, the brainstem is essential for normal regulation of core temperature. Lesions in this tissue impair the responses to thermal stress (KANEMATSU et al.,

1967; LEVKOVSKY et al., 1968; MILLS & HEATH, 1972 b). Based on these observations and on the evaluation of deep body thermosensitivity in birds we can at best only caricature the neural network controlling the thermoregulatory responses. Furthermore, the effort is less convincing in birds because the effects of changing the brainstem temperature are weak and even paradoxical. Referring again to Fig. 1 and considering the ontogeny of each of the many thermoregulatory responses, it seems plausible to suggest that each response may have its own separate set of neural elements from the receptor to the responding organ. There is increasing evidence that the characteristics of the neural network which activates a behavioral response differ in detail from the network for an autonomic response (CABANAC, 1975; SCHMIDT, 1978). Furthermore, it seems likely that each of the different responses within these two classes of responses may each differ in detail from the others within the same class. It does not seem possible to account for the differences in threshold and thermal sensitivity of the many responses based on a single controlling network for all responses. Therefore, we hypothesize that during the phylogeny and ontogeny of the thermoregulatory responses, a separate set of neural elements may have been assembled for different responses.

Considering further the neural elements as depicted in Fig. 1, it is apparent that the responses which limit the rise in core temperature above optimal temperature must have threshold temperatures for activating each response and they must increase proportionally as core temperature increases. Likewise, it is apparent that those responses which limit the fall in core temperature must each exhibit their own threshold temperature and must increase proportionally as core temperature decreases. It is conceivable that both the cutaneous and the peripheral core cold receptors exhibit threshold activities at or near optimal temperature and increase activity with decreasing temperature. In birds, only the firing rates of thermoreceptors in the beak of pigeons (NECKER, 1972, 1973) and bill of ducks (GREGORY, 1973; LEITNER & ROUMY, 1974) have been investigated. Nothing is known about the firing rates of core receptors which are peripheral to the CNS in birds.

Considering the "cool" and "warm" neural pathways leading from the peripheral cutaneous and core thermoreceptors to the motor neurons controlling effector activity, we feel compelled to hypothesize, Fig. 3, that activity in the "warm" neural pathway is inhibited by activity in the "cold" neural pathway; and similarly, activity in the cold pathway is inhibited by the activity in the warm pathway. With these crossover inhibitions, it is easy to imagine how the threshold temperatures for the antagonistic warm and cold responses are generated by the neural network. It is also easy to imagine how the threshold temperatures for the warm responses are above the optimal temperatures whereas the threshold temperatures for the cold responses are below the optimal temperature in varying degree. Furthermore, as NECKER & RAUTENBERG (1975) demonstrated, deafferenting the cutaneous input by cutting the dorsal roots in pigeons did not lessen shivering in a cold environment compared with the shivering in intact birds. However, the core temperature was less in these deafferented pigeons which would have stimulated thermosensitive spinal neurons. We further hypothesize that the neural network for a thermoregulatory response is, in essentials, the same for one response as for another and is basically the same in birds and in mammals. Of course, there are differences in the details in the network for different birds as for different mammals. The principle differences seem to be in the Q_{10}'s or temperature sensitivities of the interneu-

rons in each pathway. There may also be differences in the proportion of warm and cold peripheral receptors amongst birds as well as amongst mammals. There may be differences in the extent of the crossover inhibition at lower levels in the CNS than that represented in Fig. 3. These differences have not been investigated.

Finally, we shall illustrate with one example how the weak and even paradoxical response to changing the brain temperature can be explained in birds thus far investigated. To explain the paradoxical inhibition of shivering in Fig. 2, suppose the Q_{10} of the hypothalamic motor neuron which controls shivering is very high. Thus, even though that neuron is appropriately facilitated by hypothalamic cooling of all the neurons in the preoptic and hypothalamic nuclei, as indicated in Fig. 3, its firing rate will be reduced due to its very high Q_{10} and due to the cooling. Paradoxically reduced vasoconstriction of wing vessels of the penguin induced by hypothalamic cooling can be similarly explained. Other weak and paradoxical responses to altering hypothalamic temperature in birds may be explained by considering the relative temperature sensitivities of the neural elements in both pathways of the regulatory network.

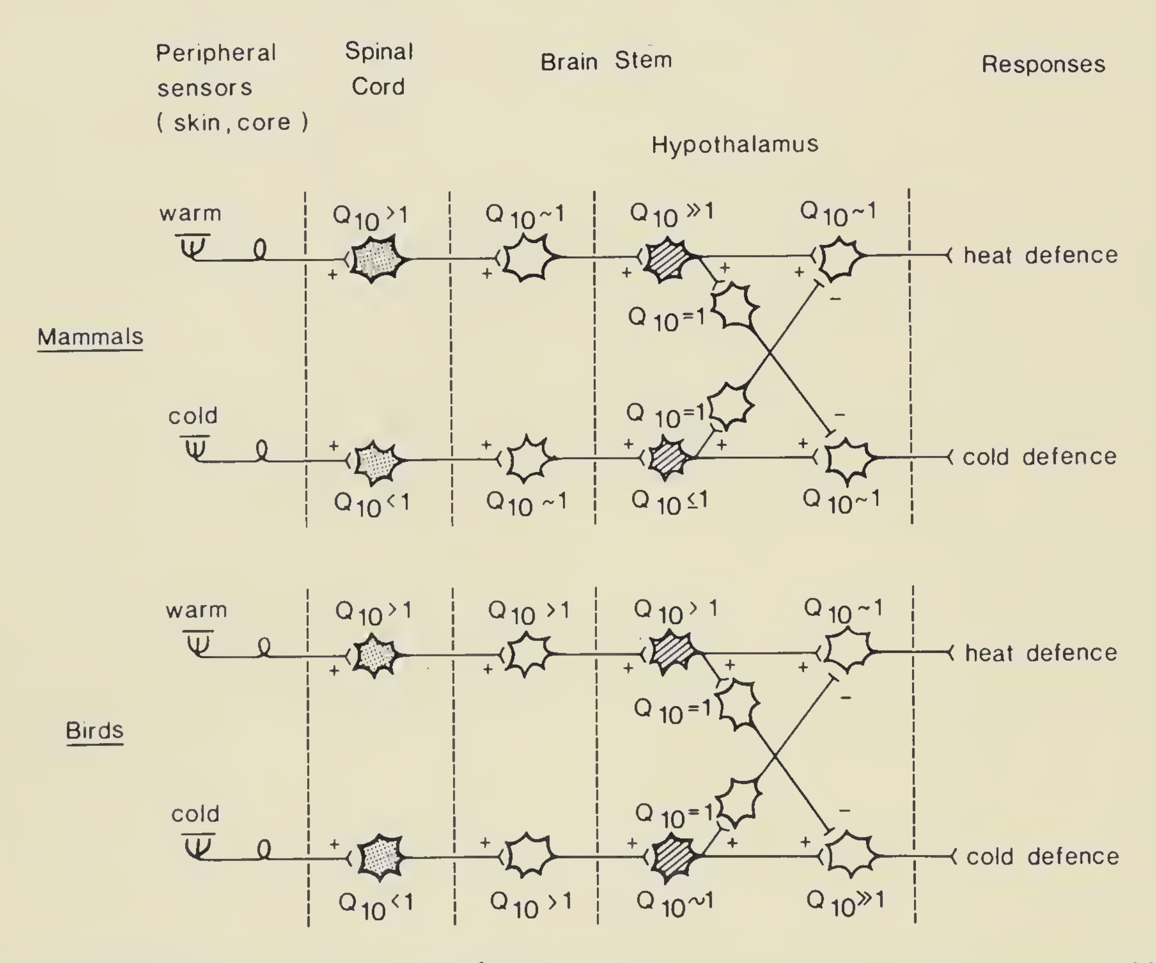


FIGURE 3. Hypothetical neural networks for regulating body temperature in mammals and birds.

These investigations in birds have taught us to be more concerned about the Q_{10} of the effector neurons situated in the hypothalamus. These effector neurons include not only those subserving thermoregulatory responses, but also those associated with osmoregulatory responses (HAMMEL et al., 1976; SIMON-OPPERMANN et al., 1978).

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SYMPOSIUM ON CIRCULATION AND RESPIRATION

9. VI. 1978

CONVENERS: H. R. DUNCKER AND K. JOHANSEN

Aspects of Cardiovascular Function in Birds

K. Johansen

Unlike the lung the avian cardiovascular system does not differ fundamentally in its structure and function from that of mammals. This does not imply that the comparative physiologist interested in heart and circulation is not challenged by conditions in birds, but the challenge lies more in how the cardiovascular system subserves and adjusts to behavioural acts and environmental exposure, which may be specialized or accentuated in birds.

I will emphasize 3 areas in which the performance of the cardiovascular system is especially important and heavily taxed in birds. These are:

(1) Cardiovascular function during physical activity. In birds this means above all flight, but many birds are also good runners, walkers and swimmers.

(2) Cardiovascular adjustment to reduced O_2 availability, a situation confronting birds at high altitude as well as habitually diving birds.

(3) The role of the cardiovascular system in the regulation of body temperature.

Cardiovascular function during physical activity

Birds have a higher heart weight in relation to body size than mammals and the systolic and mean systemic arterial blood pressure is higher and the pulmonary arterial pressure lower. The vascular resistance in both principal vascular circuits are less than in mammals (Jones & Johansen, 1972). Among birds, good fliers may increase the O_2 requirement 12—14 times during flight. For the pigeon, wind tunnel experiments have suggested that cardiovascular compensation may take on 4 to 5 times of a 10 fold increase in O_2 delivery (Butler et al., 1977). The primary adjustment for increased circulatory transport in the pigeon was an increase in heart rate rather than stroke volume much like in mammals and unlike conditions in many lower ectotherm vertebrates. Heart rate regulation in birds is held to be particularly acute since the synergism of negative (vagal) and positive (sympathetic) chronotropism is equally balanced during rest, giving a maximum potential for rate adjustment (Johansen & Reite, 1964). While in mammals the resting parasympathetic influence dominates the sympathetic, birds have a high resting sympathetic tonus to the heart.

Hummingbirds are likely to hold most metabolic records among vertebrates. Heart rates of $1200 \cdot min^{-1}$ have been recorded immediately postflight in two species (Lasiewski et al., 1967), but even higher values during flight are likely. The relative heart rate change from rest to exercise is, however, less in smaller birds (2 × resting) than in larger (3 to 5 × rest). Cardiac outputs can be estimated as high as 4770 ml · kg · min in a 10 g hummingbird which is likely to be 5 fold that of a mouse (Berger, unpublished).

Flightless birds must depend on running, walking and swimming for locomotion. Again scarcity of data precludes generalizations. A study employing telemetry tech-

Department of Zoophysiology, University of Aarhus, DK 8000 Aarhus C, Denmark.

niques for recordings of heart rate, carotid and femoral blood flow in the penguins *Pygoscelis papua* and *P. adeliae* (MILLARD et al., 1973) showed that during free roaming (running) heart rate doubled from 90 to 180 beats · min^{-1}, while femoral blood flow rose 4 times the resting value. Mean systemic arterial blood pressure increased from 80 to 125 mm Hg and femoral vascular resistance decreased by 70 %.

Swimming at the surface resulted in higher heart rates than running on land reaching about 230 beats · min^{-1}. Femoral blood flow increased far less than during running which is not surprising since swimming is powered principally by the front flippers.

Resting blood flow to skeletal muscle in birds is reported high, being 3—5 times the resting values for mammals (FOLKOW et al., 1966). This will give birds a large venous O_2 reserve for exercising muscles with less dependence on blood flow redistribution for swift changes in the activity level.

Circulation time from lungs to tissues is not known for birds. For comparative purposes we may, however, estimate how fast the entire circulating blood volume will pass through the heart.

In a resting mouse *(Perognathus longimembris)* (BW 8.3 grams) a calculation of cardiac output by the FICK principle and circulating blood volume as 8 % of body weight, gives a turnover rate of 3.5 × per minute for the blood volume when assuming the a-v O_2 difference to be 10 vol %. A resting hummingbrid *Colibri coruscans* of 8 grams passes the blood volume through the heart 10 × per minute based on the same assumptions. If we use data on O_2 uptake during flight (BERGER, 1974) and assume an expanded a-v O_2 content difference of 15 vol %, we get the incredible result that the hummingbrid passes the entire blood volume through the heart every second. A flying pigeon (BUTLER et al., 1977) has a corresponding figure of about 30 × per minute or 2 seconds for passage of one blood volume. Data for an ostrich obtained immediately after running give a value of 2.4 × per minute or 25 × slower blood passage than the hovering hummingbird. This in effect means that the hummingbird can deliver 25 × more O_2 to the tissues per unit time compared to the running ostrich. The obvious advantage of being small with much shorter distances for blood to travel is strikingly clear from this comparison. A circulation time of 1 second for the entire blood volume to traverse the systemic or pulmonary circuit, invites questions as to the kinetics of the diffusive and chemical reactions involved in gas exchange and transport.

Cardiovascular adjustment to reduced O_2 availability

Birds like other vertebrates inhabit high altitudes. Their power of flight and migration routes across mountain ranges carry many species to record altitudes exceeding 8000 m. This feat clearly surpasses what mammals tolerate even at resting conditions. The cardiovascular system must play a part in the success of many birds to perform at high altitudes. Heart rate in birds during hypoxic breathing is kept close to control values even at arterial PO_2 levels of 37—45 mm Hg. The adverse effects of the pulmonary hypertension typically associated with high altitude exposure in higher vertebrates appears much less in birds than mammals.

In a recent comprehensive study of pigeons investigated at simulated altitudes corresponding to 4000 m BOUVEROT et al. (1976) showed a cardiac output 50 % higher than a calculated value for a similar sized mammal while stroke volume was 2.75 × higher.

At such levels of hypoxia, mammals typically have a tachycardia so great as to encroach on the stroke volume and give a reduced cardiac output.

Diving birds generally practice short-lasting (less than 2 minutes) and shallow dives and thus have different requirements than the typical diving mammal or reptile.

Nearly all physiological information on diving birds have, however, been obtained during restrained submersion usually by immersion of the head only. Such information may be totally misrepresenting what goes on in natural dives, which are not only voluntary but are typically associated with physical activity like swimming and foraging. Some birds like penguins (MILLARD et al., 1973) likely have energy requirements 3—4 times resting on land when they perform their typical dives.

The apnea that must accompany submersion in the diving animal reflexly triggers a series of cardiovascular changes including a profound bradycardia geared primarily to redistribute the circulating blood, resulting in reduced O_2 requirements and improved economy of the O_2 stores. The cardiovascular changes are modified and modulated by chemo- and baroreceptor influences as well as by local metabolic factors as the dive progresses. Higher central nervous activity conditions the course of the physiological adjustments to entry and recovery from diving (JONES & JOHANSEN, 1972; PURVES, 1975). The greatly reduced cardiac output during diving and a nearly unchanged blood pressure result in a greatly increased systemic peripheral resistance. The cardiovascular adjustments are first of all important by securing the needed O_2 to organs like the brain, heart and some sensory and endocrine organs, while other organs, primarily skeletal muscle, the gastrointestinal tract and skin tolerant of temporary O_2 deprivation are under-perfused (JOHANSEN, 1964).

In a recent study on two species of penguins, *Pygoscelis adeliae* and *P. papua*, radiotelemetry was utilized to transmit cardiovascular information from freely swimming animals (MILLARD et al., 1973). During voluntary dives, bradycardia was always evident, although to a lesser degree than in restrained and submerged birds. Frequently, an anticipatory increase in heart rate preceded emersion and breathing, particularly towards the end of the longer breath-holding periods. Femoral arterial flow was reduced by no more than 50 % and did not fall to zero between beats as was observed during forced dives. During dives, the carotid flow decreased although proportionately not as much as femoral flow and never below the values recorded when the birds were on land. A rapid increase in carotid flow, particularly by a markedly increased diastolic flow component, occurred promptly in anticipation of surfacing. Reduction in arterial O_2 tension and concurrent decrease in arterial p_H were far more pronounced during forced dives than during voluntary diving. Free-dive studies on penguins suggest that the quality of the diving responses are in accord with the responses to forced diving, but the magnitude of the latter indicates the need for caution when discussing the physiological implications of the responses.

Cardiovascular regulation of body temperature

Among the endotherms, birds have the highest body core temperature and a high and rapidly changing metabolism, calling for effective temperature regulating mechanisms. The cardiovascular system plays an indispensible role in transport, dissipation and conservation of heat. In hot environments imposing a positive heat load, heat dissipa-

tion occurs by conduction and convection from the normally naked feet of birds and by evaporative cooling from the upper respiratory tract during panting and gular flutter. Exposed to a high radiant heat input birds may reduce heat entry by vasoconstriction of skin vessels in the naked feet and legs (heat vasoconstriction) (MURRISH & GUARD, 1974). Also in birds heat exchange between arterial and venous blood in specialized vascular retia in the orbital circulation with vascular connections to the brain as well as to the eye and naso-pharyngeal passages keep brain temperatures below the highest core temperature during severe heat stress (KILGORE et al., 1976).

Severe cold exposure calls for regulated responses of the peripheral circulation to reduce heat loss by vasoconstriction while the same peripheral tissues when in danger of freezing must vasodilate to prevent tissue damage and keep the tissues viable with nerves, muscles and sensory structures required to function at great variations in tissue temperature.

Blood flow to birds' feet may change in the order of 300 to 400 times through the agency of closing or opening the a-v anastomoses serving as bypasses of the nutritional capillaries of the leg tissues. Their 10 times greater diameter and investment in muscular, richly innervated vessel walls, offer structural basis for the highly variable flow.

A high blood flow is needed for dissipation of heat in heat stressed birds. When ambient conditions are conducive to heat dissipation by conduction and convection the a-v anastomoses dilate and the massive increase in blood flow is directed through these low resistance shunts and channeled back to the central venous circulation in superficial skin veins where continued heat loss may occur. At such times little blood flow is directed back from the feet through discrete rete mirabile, or through less specialized arteriovenous associations (FROST et al., 1975). The retia and the arteriovenous associations function as counter current heat exchangers when heat conservation is called for by precooling arterial blood and rewarming the venous return to prevent heat loss.

Temporal high blood flow to the naked feet of birds may occur on severe cold exposure when these tissues are in danger of being damaged by freezing. Such blood flow securing prevention of freezing while retaining viability of the tissues is also controlled by a-v shunt flow (JOHANSEN & MILLARD, 1973). In regards to control mechanisms consensus is present to the effect that an active neurogenic vasodilatory mechanism exists to specialized skin areas of some birds. Studies on birds from temperate regions have yielded results suggesting an alternative control mechanism. Based on perfusion of intact or isolated duck feet, MILLARD & REITE (1975) and REITE, MILLARD & JOHANSEN (1977) presented results to show that sympathetic nervous control is absent or weak in the web of the foot at temperatures below 8 °C. Any stimulus increasing the levels of adrenaline and noradrenaline in the blood or causing a general increase in sympathetic vasoconstrictor nerve activity produced vasoconstriction mainly if not only in the warmer tissues. The resulting rise in blood pressure caused a blood flow increase in the distal part of the ice-water immersed foot. This mechanism for local blood flow increase is not operable in warm tissues where vasoconstriction will affect the resistance along the entire foot vasculature. The usefulness of controlling blood flow through cold-exposed tissues without depending on local control mechanisms is obvious. A locally induced vasoconstriction at low temperatures could be so long-lasting

that damage might follow. The only alternative would be to have an additional local vasodilating mechanism like that demonstrated for polar birds.

The legs of birds are also essential as heat dissipators during the increased heat production of flight or other physical activity. In one study direct measurement of leg blood flow during flight of herring gulls (BAUDINETTE et al., 1976) it was shown that 80 % of the total heat production during flight was lost from the feet. In birds evaporative cooling occurs by panting or gular flutter (RICHARDS, 1970). One important aspect of panting: the magnitude and control of blood flow to the evaporating surfaces have not earlier been reported on.

In preliminary studies carotid blood flow in ducks could increase 4—5 times while heart rate remained unchanged, but breathing rate increased 20 times or more. This blood flow change was clearly related to the change in rate of breathing and is most certainly related to transportation of heat to the evaporating surfaces of the upper respiratory tract in the panting bird.

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Functional Anatomy of the Respiratory System

Hans-Rainer Duncker

Introduction

The avian respiratory system is unique among vertebrates with its differentiation into the rigid lung for gas exchange and the air sacs for ventilation of the lungs. This differentiation depends on the subdivision of the body cavity by septa. This structural and functional specialization in birds is derived phylogenetically from the heterogeneous lung of higher evolved reptiles and the constant related coelomic subdivision of a pleural cavity (Duncker, 1978 a, c, d). In the multicameral lung the chambers originate from one intrapulmonary bronchus, often in three rows, the dorsal and medial ones being highly partitioned with a large exchange surface, whereas the ventral and lateral chambers possess a larger exchange surface only near the bronchus, the distal portions being extended into dilatations for primarily non-respiratory functions. These lungs are fused with the thoracic body wall and with the postpulmonary septum which separates the pleural from the peritoneal cavity.

Body cavity subdivision and topography of lung and air sacs

The avian pleural cavity lies in the dorsal thorax, extended so far dorsally beneath the transverse processes of the vertebral bodies that the ribs incise deeply into the dorsal part of the cavity and the lungs. The dorsolateral wall of the cavity is formed by the ribs and the intercostal musculature, the medial wall by the vertebral bodies and their ventral processes, and the ventral wall by the horizontal septum (Duncker, 1971, 1980). This septum is derived from the postpulmonary septum of reptiles, which is split in embryological development by invasion of the air sacs into the horizontal septum ventral to the lungs and by the oblique septum which separates the air sacs from the intestines (Duncker, 1978 b). The horizontal septum at its lateral margin contains the Mm. costoseptales, derived from the intercostal musculature. These muscles dilate in the inspiratory phase and contract during expiration (Soum, 1896; Fedde et al., 1964), thus compensating for volume changes of the pleural cavity which are already very small due to the extreme dorsal position. The lung is fused with the walls of pleural cavity, guaranteeing the volume-constant extension in both respiratory phases.

The subpulmonary cavity, which is not a coelomic subdivision (Duncker, 1980), is lined laterally by the body wall and medially by the oblique septum, and is ventrally fixed at the sternum near its lateral margin. Only in song birds the oblique septa of both sides are united above the sternum, forming a sac-like cavity for the liver and esophagus. The subpulmonary cavity, lateral and behind the pericardial cavity, is occupied by the cranial thoracic air sac, and further caudally by the caudal thoracic air sac which extends caudally to varying degrees in different families thus displacing the fixation of the oblique septum to the lateral abdominal wall caudally. The subpulmonary cavity extends secondarily cranial to the pericardium by the development of the

Zentrum für Anatomie und Cytobiologie der Justus-Liebig-Universität Giessen, Aulweg 123, D-6300 Giessen, Bundesrepublik Deutschland.

unpaired clavicular and the cervical air sacs. In contrast to both thoracic air sacs, which alone entirely fill the posterior subpulmonary cavity, the clavicular and cervical air sacs surround the esophagus, the trachea and its muscles, nerves and vessels. The latter are fixed to the walls of the air sacs by thin membranes, which remained between the out-growing air sacs or their single diverticula.

The abdominal air sac is the only air sac located outside the subpulmonary cavity, with one exception found in kiwis in which it represents the most caudal air sac in the subpulmonary cavity. At the caudal lung margin the ostium of the abdominal air sac penetrates the non-split horizontal and oblique septa, and the air sac spreads out in the dorsal peritoneal cavity. In most birds, the wall of the abdominal air sac is fused with the dorsal and dorsolateral body wall covering the kidneys and the testes, but not the left ovary in females, except in penguins and rheas which show very limited areas of fusion. From this area of adhesion the very extensive but thin wall of the air sac spreads between the loops of the intestine. This is in contrast to the air sacs in the subpulmonary cavity, the walls of which are totally fused with the cavity walls or the structures which are surrounded by them. This is due to the fact that the subpulmonary cavity is not a coelomic cavity, originating only by the splitting of the postpulmonary septum.

The bronchial system of the paleopulmo

Immediately after penetrating the horizontal septum, the primary bronchus gives off the four medioventrobronchi (abbreviated: ventrobronchi) which ramify and spread on the ventral lung surface directly above the horizontal septum up to the cranial and medial lung margin where they bend onto the dorsolateral or medial lung surface. After reaching the dorsolateral lung surface without further bronchial branching, the primary bronchus gives off dorsally the seven to ten mediodorsobronchi (dorsobronchi) on its dorsally-arched course towards the caudal lung margin. The openings of the dorsobronchi are oriented caudally and the first four or five are closely located one above the other so that only thin, but rigid membranes separate their openings. The first dorsobronchi ramify repeatedly but decreasing regularly to the last bronchus which is without branches. They spread at the dorsolateral lung surface and bend onto the medial lung surface and at the caudal lung margin. Opposite the dorsobronchi, the lateroventrobronchi (laterobronchi) originate from the primary bronchus with their openings also directed caudally. The first laterobronchus is large and opens into the posterior thoracic air sac; a few smaller ones lie at the lung surface beneath the primary bronchus. The walls of the ventro- and dorsobronchi are very thin, lacking considerable amounts of smooth musculature and being free of any cartilage. They would collapse without adhesion to the walls of the pleural cavity. The primary bronchus is supported by cartilage half rings only up to the origins of the ventrobronchi. The further wall up to the caudal lung margin as well as the large laterobronchus possess only longitudinal and well developed circular musculature.

The long parabronchi originate in large numbers from the entire internal surface of the ventro-, dorso- and laterobronchi. Those from the ventrobronchi run towards parabronchi from the dorso- and laterobronchi, anastomosing in a median plane between them, always one parabronchus with two or three from the other side. In most species the parabronchi possess interconnections immediately after their origin from

the secondary bronchi. Thus, the first and second ventrobronchi are connected with the first, second and part of the third dorsobronchi, whereas the following dorsobronchi and the small laterobronchi are connected to the third and fourth ventrobronchi. The parabronchi are oriented more perpendicular in the anterior part, but more oblique from dorsolateral to medioventral in the posterior part of the lung, thus maintaining the same length between the secondary bronchi throughout the lung. This "paleopulmo" (Duncker, 1971) is found in all birds. The A. pulmonalis enters the lung hilus cranial to the primary bronchus and ramifies between the parabronchi, supplying all parabronchi with a large number of arterioles equally over their entire length (Duncker, 1974). The venules originate in a similar way from the parabronchi, collected by branches of the V. pulmonalis which leaves the lung hilus behind the primary bronchus.

The air sac connections of the lung

The anterior air sacs are connected to ventrobronchi: the cervical air sac to a cranial branch of the first ventrobronchus, and the unpaired clavicular and the anterior thoracic air sacs medial to the lung hilus to a short, branched stem out of the proximal third ventrobronchus. Additionally, these latter two air sacs possess ostia at the lung margin lateral to the hilus. These ostia open into the parabronchial net, which is connected to the lateral branches of the first and second and to the fourth ventrobronchi. Direct branches of the ventrobronchi to the lateral ostia only exist in a few families. In contrast, the posterior air sacs are connected directly to the posterior primary bronchus. The posterior thoracic air sac is connected by the first and large laterobronchus, and the primary bronchus opens at the caudal lung margin into the abdominal air sac.

The respiratory movements induce volume changes which act on the air sacs simultaneously. By the special arrangement of the secondary bronchi originating from the primary bronchus as well as of the air sac connections an unidirectional flow of air through the paleopulmo is generated aerodynamically. This flow pattern was first described by Hazelhoff (1943); it has been confirmed using different methods by Scheid & Piiper (1971), Scheid et al. (1972), Bretz & Schmidt-Nielsen (1971), Brackenbury (1971) and Bouverot & Dejours (1971), and is discussed by Scheid (this symposium).

The neopulmo and its connections

Only in some birds does the paleopulmo make up the entire lung, e.g. in emus and penguins. In most birds an additional connection from the primary bronchus to the posterior air sacs by a parabronchial net has been developed. This is very small in storks and cranes, somewhat larger in gulls and ducks and most extensive in galliform and song birds. Several parabronchi originate from the lateral side of the primary bronchus, the proximal dorsobronchi and the laterobronchi, interconnecting into a meshwork which opens laterally into the ostia of the posterior thoracic and abdominal air sacs. These ostial openings can be elongated as saccobronchi in some species. When this "neopulmo" (Duncker, 1971, 1972 a) is developed extensively, as in galliform and song birds, it totally substitutes for the connection of the primary bronchus to the abdominal air sac. In contrast, the posterior thoracic air sac always maintains its large

laterobronchus in addition to its neopulmonal connection. The air sac ostium has been separated in song birds from that of the neopulmo. The air flow through the neopulmo alters its direction according to the respiratory phase, in contrast to the paleopulmo. As yet unknow is the exact route of the air through the anterior part of a highly developed neopulmo which by a secondary substitution of the lateral branch of the first dorsobronchus attained a connection to the lateral ostia into the clavicular and anterior thoracic air sacs.

The parabronchi and their air capillary - blood capillary meshwork

The parabronchi are long tubes with open connections at both ends with the secondary bronchi or air sac ostia. Their lumen, 200—500 μm in diameter, is lined by an interconnected circular or hexagonal meshwork of smooth muscle bundles. These bundles, 100—300 μm apart, surround the atria which are 100—300 μm deep, and which are separated from one another by very thin septa. In these septa and around the muscle bundles elastic fibers are abundant, but are lacking in the further parabronchial wall. The well innervated muscles and the elastic fibers form a functional system for varying the luminal diameter. From the peripheral side of each atrium a few funnel-shaped infundibula originate, running radially into the 200—500 μm thick parabronchial mantle and giving off over their entire length several air capillaries, ranging from 3 to 10 μm wide in different species. They surround the blood capillaries, forming a three dimensional, interconnected meshwork. The blood capillaries originate from the arterioles in the interparabronchial septa in great numbers at short intervals, running, slightly curved, towards the parabronchial lumen. Here they are collected beneath the atria by small venules, which are drained by small veins into the interparabronchial veins. The blood capillaries in the parabronchial wall lack interconnections as in the capillary nets of reptilian or mammalian lungs. The blood capillaries are intermingled with the air capillaries, making up the exchange surface, which is regularly more than ten times that of an equal volume unit in the lung of a mammal of comparable body size (Duncker, 1973).

The blood capillary - air capillary meshwork is only existent in a rigid, volume constant lung. The diameter of the air capillaries is so small that the radius-dependent surface tension is much higher than in mammalian alveoli. The well developed "surpellic film" (Pattle, 1978) reduces the surface tension, but only to such a degree that no transsudation of serum out of the blood capillaries can occur. If the lung were volume-variable, the air capillaries would collapse and could not be re-inflated. Only the lumina of the parabronchi are ventilated by the respiratory air flow. In the atria and in the air capillaries gases are exchanged by diffusion only which may be the limiting factor for the maximal thickness of the blood capillary - air capillary network, which in no species exceeds 500 μm. Even in the largest birds the total parabronchial diameter is maximally 2 mm. In smaller and very active birds the parabronchial diameter decreases with a strong reduction of the atrial zone, but parabronchi smaller than 500 μm are not found.

The developmental conditions of the lung

The air capillaries depend on the rigid lung structure also at the moment of hatching. They cannot be inflated. One to three days before hatching, according to the incuba-

tion length, the embryo ingests the amnion fluid and breaks the membrane of the air space, aerating the amnion and initiating regular respiratory movements. Thus, the air sacs and the bronchial system including the tubular parabronchi are aerated. At this time all secondary bronchi and parabronchi according to their number and position as found in adults are developed (Duncker, 1972 b, 1978 b). Under air respiration the first layer of air capillaries develops around the growing blood capillaries, making up the first respiratory exchange network, relatively thin in altritial and thicker in precocial birds. At the beginning of the air capillary development the gas exchange is fully maintained by the chorioallantoic membrane, increasingly taken over by the developing lung until the embryo hatches. For the development of the functional capability of the lung this overlap of chorioallantoic function and respiration of air is necessary, and therefore birds could not develop viviparity in phylogeny because of the highly complicated structure of their respiratory system.

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Ventilation and Gas Exchange in the Lung

Peter Scheid

Introduction

The structure of the avian respiratory system is markedly different from that of other vertebrates, particularly from the well-studied mammalian alveolar lung. The most conspicuous differences are (1) the segregation of the gas exchanging parabronchi from the air sacs which like bellows provide the ventilatory flow; and (2) the structure of the parabronchi as long tubes, open at both ends, and contacted by blood capillaries all along their length. These structural pecularities are complemented by functional characteristics, which pertain to both ventilation and gas exchange in the avian lung, and some recent advances in these areas shall be briefly discussed in this paper.

Ventilation of the lung

Direction of ventilatory flow through the parabronchial lung

In birds, like in most land-dwelling vertebrates, ventilatory gas flow is provided by the action of respiratory muscles, expanding and compressing the rib cage and the underlying compliant tissue of the respiratory system, which thus constitutes a reciprocating pump for convective air movement in and out the bronchial arrangement. In mammalian lungs the alveoli constitute a dead-end for this ventilatory air flow, and it is thus evident that the direction of air flow in the bronchi must be reciprocating in inspiration and expiration. The avian parabronchi, however, are tubes which are open at both ends and thus offer the possibility of flow in either direction. It has accordingly long been debated (1) if there is parabronchial gas flow during both respiratory phases, inspiration and expiration; and (2) in which direction this flow passes through the parabronchi (cf. Sturkie, 1965; Scheid & Piiper, 1971; Piiper & Scheid, 1973).

The controversial arguments had all been based on rather indirect experimental approaches and observations until it recently became possible to measure the air flow direction with small flowmeter probes inserted into the bronchial system of spontaneously ventilating birds (cf. Piiper & Scheid, 1973). The results of various independent groups have unanimously shown that in the mediodorsal secondary bronchi (MD) air flows during both inspiration and expiration and that the direction of this flow is the same in both respiratory phases, viz. from the main bronchus (Mb) towards the parabronchi. Hence, the parabronchial lung is ventilated in the same direction in both inspiration and expiration (unidirectional ventilation).

Although this finding settled the controversy between the bidirectional flow theory of Zeuthen (1942) and the unidirectional hypothesis of Hazelhoff (1943), it remained unresolved if, on inspiration, gas that had passed the bronchi from MD towards the medioventral secondary bronchi (MV) would recirculate and admix with the gas flow in Mb. By continuously monitoring the gas concentrations along Mb and MV in spontaneously breathing ducks, we have recently provided evidence that there is no gas flow

Abteilung Physiologie, Max-Planck-Institut für experimentelle Medizin, D—3400 Göttingen, Bundesrepublik Deutschland.

during inspiration between MV and Mb indicating a complete valving at the orifice of MV into Mb (unpublished).

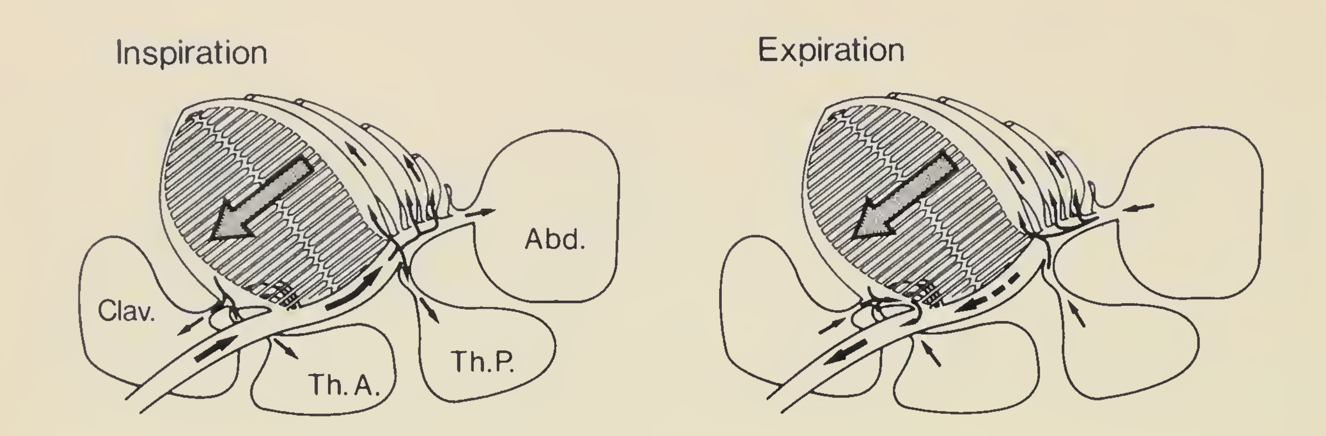


FIGURE 1 Diagram on air flow pattern in the avian respiratory system during inspiration and expiration. Still unknown is whether air flows in expiration in the main bronchus between the origins of the secondary bronchi (broken arrow).

Figure 1 shows schematically the pattern of air flow in avian lungs on inspiration and expiration. The only site in the bronchial system at which air flow has not yet been adequately investigated is the part of Mb between the orifices of MV and MD. It remains thus open if during expiration there exists air flow in this region or if all flow from the caudal air sacs is directed out via MD and the parabronchi.

Mechanisms responsible for rectification of ventilatory flow

It is tempting to assume anatomical valves that provide the unidirectional parabronchial gas flow and the absence of flow across the orifices of MV during inspiration. However, such valves have never been described. In fact, SCHEID & PIIPER (1971) have shown that MD gas flow remains unidirectional in pump ventilated relaxed animals, and also post mortem. Further experiments (SCHEID et al., 1972; BRACKENBURY, 1971, 1972) suggest that the anatomical arrangement within the bronchial system allows aerodynamical mechanisms to act on gas flow. However, the subject is not yet fully understood.

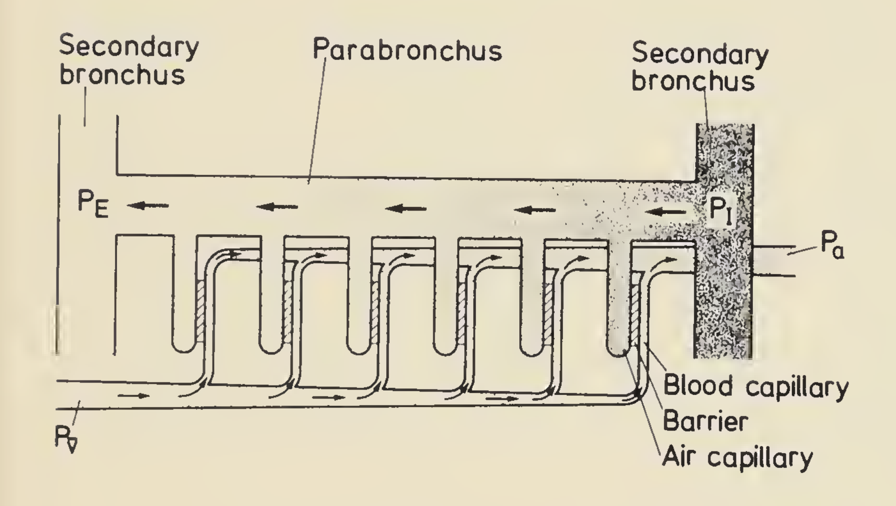
Gas exchange in the parabronchial lung

The route along which gases exchange between the parabronchial air and the pulmonary capillary blood may be subdivided into several different steps. The O_2 is brought into the parabronchial lumen by convective movement of the tidal air. Diffusion in the gas phase of the air capillaries is the only mechanism by which O_2 will be transported to the blood-gas separating membrane, which is traversed by diffusion in the liquid phase as is the plasma and erythrocyte until O_2 reaches its destination, the hemoglobin molecule. For CO_2, the same steps are taken in the reverse direction. A model of the parabronchus is depicted in Figure 2.

We will first neglect the diffusion resistance in the air capillaries and later consider its effect on gas exchange. We will further assume that the lung is functionally homogeneous so that a single parabronchus is representative of the total assembly.

The cross-current system of parabronchial gas exchange

The essential structural and functional elements of the parabronchus that have to be considered for gas exchange are the parabronchial lumen, with gas moving through, and a great number of blood capillaries which contact an only short part of the parabronchus at different sites along its length. The blood capillaries are thus arranged in parallel whereas the gas flowing through the parabronchial lumen meets these capillaries in serial order. Hence, the parabronchus is a serial-multicapillary system. The term cross-current system has also been used since the directions of gas and blood flows in the contact region cross each other. Figure 2 shows a typical profile of the partial pressure of O_2, P_{O_2}, in the parabronchial gas, the P_{O_2} declining as air moves through the parabronchus and O_2 is taken up by the blood. Hence, the blood leaving the capillaries is better oxygenated at the initial parts of the parabronchus, where the P_{O_2} is still high, than at its end.



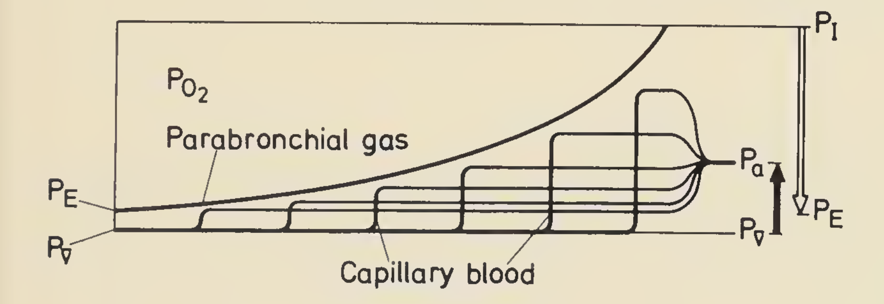


FIGURE 2 Cross-current model for parabronchial gas exchange. Top, diagram of a parabronchus with air capillaries and blood capillaries. Density of stippling indicates the concentration of O_2 in lung gas and blood, which is also shown by the P_{O_2} profiles (below).

For the arterial blood, which constitutes a mixture from all capillaries, the P_{O_2} may exceed the level in end-parabronchial gas (Fig. 2, below). This overlap of P_{O_2} ranges in blood and gas can never be achieved for alveolar lungs of mammals, where the best is an equilibrium in P_{O_2} between alveolar gas and arterial blood. The overlap reflects in fact the high gas exchange efficiency of the cross-current system of avian lungs, which means that for given ventilation, blood flow and diffusing capacity, the avian lung can transfer more O_2 to the blood than can the alveolar lung.

The overlap of gas and blood partial pressures is particularly prominent for CO_2, and it is a common experimental finding that end-expired exceeds arterial P_{CO_2}. The recent observation of expired P_{CO_2} exceeding even the mixed-venous level in spontaneously breathing birds can be explained by the peculiar role played by the Haldane effect in the cross-current system (MEYER et al., 1976).

SCHEID et al. (1978) have experimentally determined the diffusing capacity of the blood-gas membrane in resting ducks. Their value is similar to that expected for a mammal of similar size or metabolism. Their results also show a remarkable functional homogeneity between parabronchial units.

Transport of gases in the air capillaries

In many species the air capillaries are blind-ending tubules leaving thus diffusion as the only mechanism for gas transport in their gas phase. However, even in those species in which the air capillaries of neighboring parabronchi communicate, there is likely to be no pressure head that would drive a convective flow of gas through the capillaries. Thus the assumption of diffusion as the sole mechanism for gas transport inside the air capillaries seems well justified.

ZEUTHEN (1942) and HAZELHOFF (1943) have concluded from model calculations that the air capillaries offer no appreciable diffusive resistance to gas transfer. Their models may, however, be criticized as unrealistic and the results derived may thus be questioned (SCHEID, 1978). The arrangement of blood flow past the air capillaries bears similarities with the counter-current system in which two media with opposite flow directions reach gas exchange contact. In the air capillaries, however, only blood flow is convective whereas gas transport is diffusive. SCHEID (1978) has, therefore, used the term countercurrent-like system. He has calculated the limitation offered to gas exchange by the air capillaries. His conclusion is that during rest, the transport of neither O_2 nor CO_2 is appreciably limited by diffusion within the air capillaries. The limitations reside rather in ventilation and perfusion of the lung and, particularly for O_2, in membrane diffusion. During increased metabolic rates, however, as would be expected during flight, the diffusive resistance inside the air capillaries may not be neglected. Experimental results to test these calculations are still lacking.

Air flow direction and gas exchange

From the standpoint of gas exchange, there is no apparent need for the rectification of parabronchial gas flow in birds, since the gas exchange efficiency in the counter-current model is insensitive to gas flow direction (SCHEID & PIIPER, 1972). It is possible that this flow pattern is of significance for other systems. For example, the intrapulmonary CO_2 receptors which affect respiration (cf. FEDDE, this symposium) reside mainly at the caudal ends of the parabronchi and thus receive, during both phases of respiration, the gas that enters the parabronchus. It may be of significance for these receptors to be kept, during the entire respiratory cycle, at a low level of P_{CO_2} where their CO_2 sensitivity is high.

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Are Avian Intrapulmonary Chemoreceptors Involved in the Control of Breathing?

M. R. Fedde, J. P. Kiley and W. D. Kuhlmann

Introduction

Many recent advances have been made in elucidating the mechanisms involved in the control of breathing in birds. Most studies have been on birds at rest, both anesthetized and unanesthetized, but some studies on changes in respiratory pattern in flying birds have been reported. This review attempts to summarize evidence on involvement of recently discovered intrapulmonary chemoreceptors (IPCs) in controlling avian respiration.

Early observations relating to IPC action in birds

In 1881, Bieletzky demonstrated that apnea quickly occurred when a steady stream of air was passed into the trachea, through the lungs, and out to the atmosphere via openings in the thoracic and abdominal air sacs in chickens and ducks. That observation was later verified and expanded upon in many species of birds (Bordoni, 1888; Treves & Maiocco, 1905; Foà, 1911; Dooley & Koppányi, 1929; Hiestand & Randall, 1941). More recently, Van Matre (1957) suggested that the apnea produced by unidirectional ventilation of the respiratory system with air resulted from afferent impulses arising from receptors sensitive to the chemical composition of the respiratory gases and not from distortion of air passages or the thoraco-abdominal wall. Thus, the idea of an intrapulmonary chemoreceptor system which could produce a profound change in respiration when activated had been firmly established. However, direct proof of receptor location and details of receptor activation had to await more definitive experiments.

Direct evidence for IPC location and adequate stimulus

Many studies have demonstrated that afferent impulses in the Nn. vagi are important in maintaining normal breathing patterns in birds (see King, 1966 for review). However, the intrapulmonary location of chemoreceptors was not conclusively demonstrated until reflex studies using vascularly isolated lungs were conducted (Burger, 1968; Peterson & Fedde, 1968). In these studies, apnea, induced by reducing intrapulmonary CO_2 concentration in unidirectionally ventilated chickens, occurred as rapidly when all blood flow through the lungs was stopped as when blood flow was present, indicating the receptor system was intrapulmonary. The apneic response was significantly delayed after vagotomy, suggesting the afferent pathway was in the vagus.

Single-unit vagal recordings now have confirmed that: (1) IPCs are within the lung; (2) the adequate stimulus for IPCs is carbon dioxide concentration; and (3) IPCs can respond to both static and bidirectional rate changes in intrapulmonary CO_2 concentration; (Fedde & Peterson, 1970; Leitner & Roumy, 1974; Molony, 1974; Osborne &

Department of Anatomy and Physiology, College of Veterinary Medicine, Kansas State University, Manhattan, Kansas 66506 U.S.A.

Burger, 1974; Burger et al., 1974; Fedde et al., 1974 a, b; Osborne et al., 1977 b; Banzett & Burger, 1977). The IPCs have not been observed morphologically, but they appear to be in the gas exchange region of the lung, with many lying near the mediodorsal secondary bronchi (Scheid et al., 1974; Nye, 1977).

Evidence for involvement of IPCs in control of breathing

Response to airway loading with CO_2

Whether they are anesthetized, decerebrated, or unanesthetized, chickens and ducks forced to inhale low concentrations of CO_2 (up to about 3 %), increase ventilation without (or with a very small change) changes in arterial P_{CO_2} (Pa_{CO_2}) (Kuhlmann & Fedde, 1976; Osborne & Mitchell, 1977, 1978; F. L. Powell, M. R. Fedde, R. K. Gratz & P. Scheid, unpublished observations). The constancy of Pa_{CO_2} is not maintained when the vagus nerves are cut (Mitchell & Osborne, 1978). These results have been interpreted to indicate that the ventilatory increase cannot result from a change in discharge of peripheral or central chemoreceptors, which depend on an arterial bloodborne stimulus. The most likely receptor system responsible for matching ventilation to the airway-CO_2 load is the IPC system.

Ventilatory responses to stimulation of intrapulmonary and systemic chemoreceptors

Using the technique of independent ventilation of each lung in anesthetized chickens, Osborne et al. (1977 a) determined the contribution of IPCs and of systemic chemoreceptors bathed by arterial blood on the ventilatory effort. They found that respiratory amplitude increased and frequency decreased when the intrapulmonary P_{CO_2} was increased from 0 to 35 torr in one vascularly isolated but innervated lung, while Pa_{CO_2} was held constant at 29 torr. Thus, the only receptor system stimulated by the increased intrapulmonary P_{CO_2} was the IPC system in the right lung, and the reflex responses resulted in both respiratory frequency and amplitude modulation. They further found that additional increases in intrapulmonary P_{CO_2} above 35 torr in the vascularly isolated but innervated right lung had only minimal effects on respiratory movements. Such response is consistent with static response curves of IPCs to various levels in intrapulmonary P_{CO_2} (Osborne & Burger, 1974) in which the discharge frequency of most IPCs is low at a P_{CO_2} above 35 torr and is not greatly reduced as the P_{CO_2} is increased further.

Their study clearly indicated that nonpulmonary chemoreceptors also influenced ventilation. Increasing Pa_{CO_2} from 19 to 61 torr while holding the intrapulmonary P_{CO_2} in the vascularly isolated but innervated right lung constant at 21 torr also increased respiratory amplitude and decreased frequency, indicating that these receptors operate over a wider range of CO_2 stimuli than do IPCs.

Their data suggest that IPCs operate with greatest sensitivity to control breathing from the normal to hypocapnic range of intrapulmonary CO_2 concentrations and that the other systemic chemoreceptors operate most effectively to augment breathing when the bird becomes hypercapnic.

Pacing respiration with intrapulmonary CO_2 oscillations

KUNZ and colleagues have conducted experiments that indicate IPCs are important in controlling breathing. They demonstrated that the ventilatory rhythm of an awake, unidirectionally ventilated chicken will synchronize with oscillating intrapulmonary CO_2 concentrations over a range of ½ to 2 times the normal frequency of breathing (KUNZ & MILLER, 1971, 1974, 1975; KUNZ et al., 1973). Respiration in the chicken can be paced by a variety of CO_2 waveforms, and evidence suggests that the rise in intrapulmonary CO_2 concentration, which would act to inhibit the discharge of IPCs, is the important event that triggers onset of the subsequent breath (MILLER & KUNZ, 1977; KUNZ & TALLMAN, 1978). Although other chemoreceptors may also be influenced by the oscillations in intrapulmonary CO_2 concentrations, it is likely that the IPCs are most directly involved with the response.

Evidence for involvement of non-IPCs in the control of breathing

Apneic response to reduced intrapulmonary CO_2 concentration after bilateral, cervical vagotomy

When the intrapulmonary CO_2 concentration is suddenly reduced during unidirectional ventilation, vagotomized birds become apneic with a latency of approximately 5 seconds compared with a latency of about 0.5 second before vagotomy (PETERSON & FEDDE, 1968, 1971). Thus, other chemoreceptors, either peripheral (with a nonvagal afferent pathway) or central, appear to influence the central respiratory neuronal pool. The experiments of OSBORNE et al. (1977 a), previously discussed, provide more direct evidence for the presence and action of other receptors.

Carotid bodies

Denervation of the carotid bodies in ducks reduces the ventilatory response to increased inspired CO_2 concentration or to increased Pa_{CO_2} (BOUVEROT et al., 1974). Although the rapid, first-breath response to changes in inspired CO_2 concentration remains after carotid body denervation, the time required to reach the peak response is considerably longer than in intact birds. These results suggest that the carotid bodies can detect changes in Pa_{CO_2} and may influence the central neuronal pool.

Ventilatory response to exercise

Although studies have been conducted on exercising birds (BERGER & HART, 1974; FEDAK et al., 1974), very little is known about the control of ventilation during exercise. Recent experiments on flying starlings and pigeons (TORRE-BUENO, 1978; BUTLER et al., 1977) and running ducks indicate that exercise produces pronounced hyperventilation. In running ducks, the hyperventilation causes a decrease in both mixed venous P_{CO_2} and Pa_{CO_2}. Arterial p_H generally increases during exercise, apparently as a result of reduced Pa_{CO_2}; but interestingly, mixed venous p_H drops at the beginning of exercise then returns to near its resting value before the termination of exercise. These observations pose interesting questions about the mechanisms controlling breathing during exercise.

Ventilatory response to venous CO_2 loading

Anesthetized or decerebrated chickens increase both tidal volume and respiratory frequency when presented with a high venous CO_2 load in infused blood but they are unable to adjust ventilation to the added load fast enough to prevent a rise in Pa_{CO_2}. End-expired P_{CO_2} rises to a maximum within 3 to 4 breaths after beginning the infusion of the high CO_2 load but the rise in ventilation is much slower and continues for several breaths after the CO_2 load is removed. These results suggest that if the IPCs are involved in the control of breathing, they do not act fast enough to increase ventilation in proportion to an increased venous CO_2 load. It is possible, however, that the elevated Pa_{CO_2} results from shunting of blood past nonrespiratory exchange surfaces in the lungs. However, there is no current evidence for anatomical shunts in the chicken lung (ABDALLA & KING, 1976).

CO_2-sensitive mechanoreceptors in the cardiovascular system

CO_2-sensitive mechanoreceptors in the avian heart have afferent fibers in the middle cardiac nerve (ESTAVILLO & BURGER, 1973). Recent studies indicate that stimulating the middle cardiac nerve markedly depresses the amplitude of breathing (ESTAVILLO & YOUTHER, 1978). It is possible that these receptors may monitor both cardiac output and Pa_{CO_2} in a way that approximately matches ventilation to perfusion of the lungs.

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Aspects of Bird Flight Respiration

Martin Berger

Respiratory responses to flight in birds have been investigated and summarized in various contexts in recent years. I will refer to several reviews about the respiratory apparatus, respiration, flight power, energetics, and thermal relations, reviews that comprise many facts, ideas and discussions that are related to the aspects presented here: Duncker (1971), Lasiewski (1972), Calder (1974), Calder & King (1974), Berger & Hart (1974). I will not attempt to present a comprehensive treatment. It is the objective of this paper to review some recent results about respiration during flight in birds emphasizing ventilation and respiratory flow and its adjustment to flight.

Respiratory (tracheal) air flow and wing movement

The old contention that an obligatory coupling exists between wing movement and respiratory air flow (or frequency) is no longer tenable. Today we know that the respiratory movements of the rib cage that induce air way pressure changes can be independent of pectoral muscle activity. Yet there are many instances of a coupling that reach from synchrony to different types of co-ordinations (up to 5:1), and we ask where and why such co-ordinations occur.

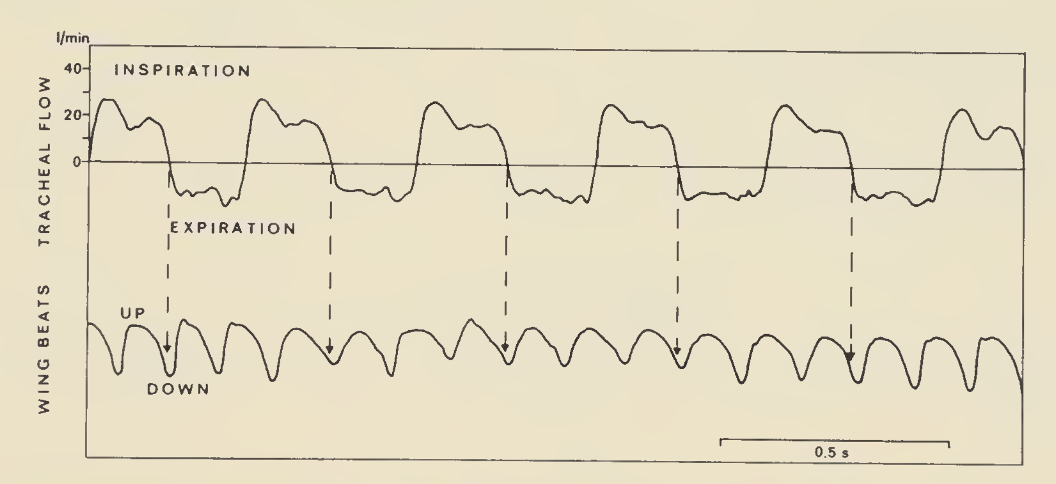


Figure 1. Simultaneous recording of respiratory flow and wing beats in a Black Duck *(Anas rubripes)*. The frequencies are clearly related in a 3:1 pattern with a constant phase relationship: end of inspiration towards the end of the downstroke.

A co-ordination is regarded present if in a breath by breath analysis, phasic relations occur between wing movement and breathing, e.g. if start of inspiration or expiration occurs only or preferentially in a certain phase of the wing beat cycle. A comparison of frequencies alone uncorrelated to the timing of the two events is not suited for evaluation of co-ordination between wing beat and ventilation.

A coupling may be expressed by many types of phasic co-ordination, from a 1:1 synchrony to a 5:1 co-ordination (5 wing beats per breath). 1:1 was found in 2 species, 2:1 only in 1, 3:1 in 6, 4:1 in 6, and 5:1 in 3 species; also 3:2, 5:2, and 7:2 may occur (Berger et al., 1970 b). A typical instance of a 3:1 co-ordination is shown in Figure 1.

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The inspiration begins towards the end of upstroke, the expiration towards the end of downstroke. This phasic co-ordination is the predominate type.

In general, wing beat rates of most birds are higher than breathing rates, so far only in pigeons (exceptional high breathing rates) and crows (low wing beat rates) a synchrony of the rates has been found. It was suggested that synchrony is present in larger rather than in small birds (TUCKER, 1968 b). But besides body size the wing area that determines wing rate has to be taken into consideration. Birds with relatively small wings (high wing loading) have relatively high wing beat rates (e.g. auks and ducks) and vice versa (e.g. crows, gulls and herons). Since large birds have in general a high wing loading due to similarity in construction we better calculate the wing loading index: (body mass)$^{2/3}$. (wing area)$^{-1}$, if we look for a figure that is related to the wing rate independent of body size. A high wing loading index (or a relatively high wing rate) is associated with high ratios of wing rate/breathing rate.

Co-ordinations may occur during take-off, horizontal unhurried flight (slow and fast), landing, ascending and descending flight. So far no flight situation can be excluded completely. However, co-ordinations were interrupted briefly or they changed from one type to another in the following situations: during turning, slow flight and take-off, and that by a few faster wing beats or by sudden changes in respiration rate from one to another level. After that the co-ordination was immediately re-established.

Looking at respiratory (tracheal) air flow in connection with the wing beat cycle (Figures 1, 3) it is obvious that upstroke as well as downstroke cause reductions in the magnitude of flow. During downstroke the inspiratory air flow is more markedly reduced than during upstroke. Flow inhibition and augmentation occurs in accordance with the following scheme:

	towards end of upstroke	mid to end of downstroke
inspiratory flow	small reduction	large reduction
expiratory flow	increase	increase
flow reversal	exp. → insp.	insp. → exp.

If wing muscles and respiratory muscles act in the same direction their effects may be added, at least the described timing will be of advantage to another timing where flow reversal is slowed down by wing muscle activity.

The rate of change of air flow in the trachea (air acceleration = steepness of flow curve) is highest during flow reversal in flight respiration. The figures from other activities are clearly lower, even from postflight where high flow values are found:

Maximal change of air flow during flow reversal at	Evening Grosbeak	Black Duck
rest	0.5 l/s^2	2.0 l/s^2
flight with co-ordination	10 l/s^2	30 l/s^2
postflight	3.5 l/s^2	12 l/s^2

The effect of an increased air acceleration is demonstrated in Figure 2. It becomes clear that with a fixed maximal air flow and constant respiration rate (or breath duration) an increased air acceleration will

(a) shorten duration of flow reversal,

(b) extend duration of maximal flow, and

(c) enlarge tidal volume (and therefore ventilation).

The two latter effects may have physiological significance for gas exchange requirements during flight. The magnitude of tracheal air flow will not only determine the magnitude of parabronchial flow. It has been suggested (DUNCKER, 1971) that there might be also qualitative differences in ventilation of gas exchange surfaces when respiratory air flow is altered. Thus there is reason to expect that the paleopulmo is ventilated only at higher air flow and therefore the effective parabronchial ventilation can be considerably augmented by a longer peak flow duration.

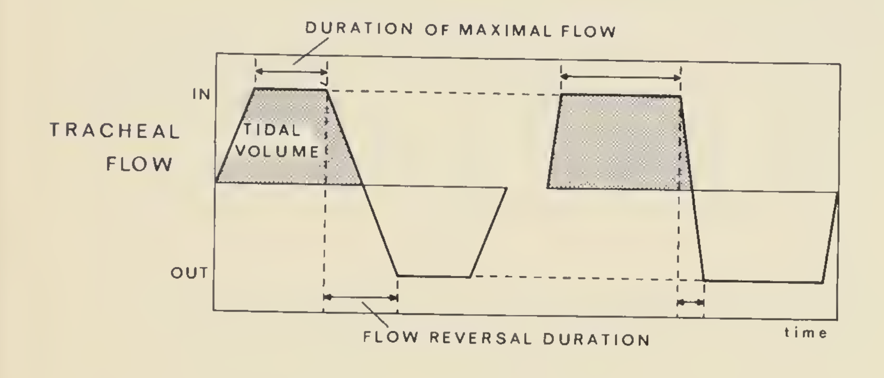


FIGURE 2. Respiratory (tracheal) flow with long and short duration of flow reversal. In either schematic instance maximal flow and breath duration (frequency) is unchanged. Short flow reversal duration leads to increased tidal volume (and ventilation) and to prolonged duration of maximal flow.

An unaltered phase relationship between time of flow reversal and wing position as described above requires uneven co-ordination numbers (1:1, 3:1, 5:1) when duration of inspiration shall equal duration of expiration. A 4:1 co-ordination, however, can be maintained with minor alterations of the described type of phasic co-ordination—at that usually inspiration duration is somewhat augmented. It may also occur (see fig. 3) that inspiration duration varies considerably (up to 61 % of breath duration) so that one breath lasts either 3 or 4 wing beats (and nothing between) in an irregular pattern, but with a fixed phasic co-ordination.

Air flow patterns at different activities

The tracheal air flow pattern in the Evening Grosbeak during flight and other activities is shown in Figure 3. When compared with pigeons, Ring-billed Gulls and Black

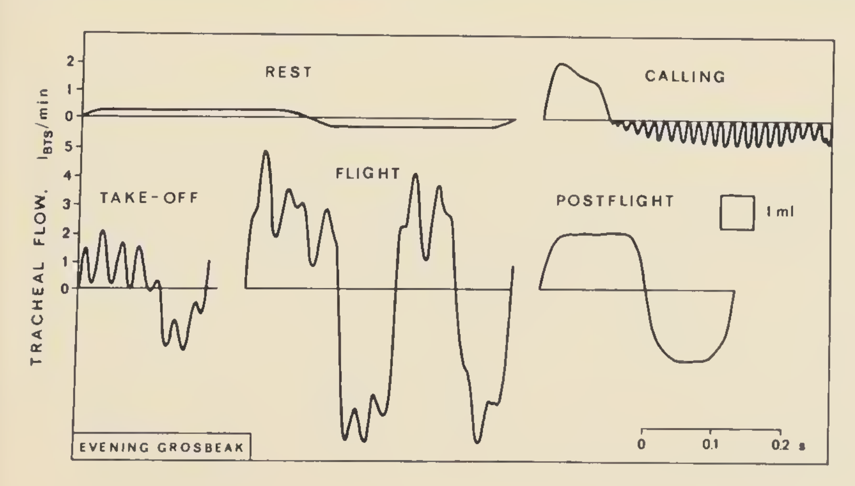


FIGURE 3. Respiratory (tracheal) flow patterns of the Evening Grosbeak *Hesperiphona vespertina* during rest, calling, take-off, flight, and postflight. The area under the curve represents the tidal volume. (From BERGER & HART, 1968; BERGER, et al., 1970 b; HART & BERGER unpubl.)

Ducks, the magnitude of respiratory air flow, tidal volume and ventilation increases with increasing body size, while respiration rate decreases (cf. Berger & Hart, 1974). For a given species, the magnitude of peak air flow increases in the succession: rest—panting—take-off—postflight—flight. The largest tidal volumes are recorded during flight and postflight (Hart & Roy, 1966; Berger et al., 1970 a). Breathing frequency is immediately changed at the onset and at the end of flight while the response in tidal volume is gradual.

Ventilation volume

Ventilation and body size

When compared on a body size basis, the respiration rate during flight in different species exhibits relatively little changes (Berger & Hart, 1974). From hummingbirds and tits to ducks and pheasants the rate decreases from 4—6/s to about 1.5—3/s. In contrast, the few data on tidal volume may increase in the same body size range from 0.5 ml to 40—100 ml. The ventilation (tidal volume × respiration frequency) increases also from about 0.1 l/min to 10 l/min; the few available data (6 species) were put together in the following regression: $\dot{V} = 42\ M^{0.73}$ ml/min (body mass M in g).

Ventilation and heat

Panting ventilation volume in rest is considerably lower than flight ventilation. In flying birds the ventilation is apparently primarily adapted to the demands of the respiratory and circulatory system to guarantee a 6—15 fold oxygen uptake compared to rest.

Flight at high temperatures is associated with increased respiratory water and heat loss (Tucker, 1968 b; Berger & Hart, 1972; Bernstein, 1976). This effect can be explained by a low temperature of expired air at low ambient temperatures and vice versa, as well as by altered ventilation volume. In Fish Crows (Bernstein, 1976) it was shown that when ambient temperature increased from 20 to 28°C, also tidal volume (from 15 to 23 ml) and ventilation was increased (from 1.8 to 3.0 l/min). In Budgerigars (Aulie, 1975) a very high respiration frequency of 16/s being suggestive of panting was measured at high T_B. In contrast, hovering hummingbirds (Johansen & Berger, unpubl.) did not show any sign of panting in flight where under heat load respiration frequency can increase from 5 to 7/s. If sitting overheated birds which were heavily panting were brought to flight respiration rate decreased immediately.

Ventilation and altitude

Resting birds increase their ventilation volume (BTPS) when exposed to altitude conditions (low barometric pressure, low oxygen pressure) (Tucker, 1968 a; Bouverot et al., 1976). During flight at altitude the power input (oxygen uptake) in hovering hummingbirds is increased (Berger, 1974). Flight ventilation measurements at altitude are available only from hovering hummingbirds, too (at high ambient temperatures, Berger, 1978). The increased ventilation (BTPS) that was found at 4000 m altitude in comparison to sea level conditions could not explain the whole increase in oxygen uptake. Therefore an increase in oxygen extraction from ventilated air was assumed.

This paper is dedicated to the memory of J. S. Hart (1916—1973) who opened and contributed significantly to the field of avian physiology.

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Ontogenetic Development of Respiration in Birds

Jens Peter Lomholt

Bird embryos develop inside a hard calcareous egg shell, which protects the embryo against mechanical injury as well as against excessive dehydration. The shell is thus necessary for the normal development of the embryo during incubation by the parent in a nest. The existence of this shell, so crucial to the protection of the embryo, must present a limit to the respiratory gas exchange. If the shell is to restrict evaporation from the egg, it must at the same time constitute a barrier to the transport of the respiratory gases, oxygen and carbon dioxide.

This paper discusses various aspects of how the respiratory requirement of the embryo, confined within an egg shell of limited surface area, can be satisfied throughout the period of incubation in spite of the very large increase in metabolism which occurs as a result of the growth of the embryo (Romijn & Lokhorst, 1960; Romanoff, 1941; Hoyt et al., 1978).

The exchange of respiratory gases across the egg shell is believed to occur solely by diffusion, i.e. the gas exchange does not depend on the convection of air around the egg. One type of evidence for this is the common experience that the evaporative loss of water from eggs during artificial incubation is independent of air velocity in the incubator and is only influenced by the humidity of the air (Lundy, 1969).

Exchange by diffusion across a boundary depends on the area and permeability of that boundary and on the concentration difference between the two sides of the boundary. The barrier to the diffusion of oxygen and carbon dioxide between the ambient air and the vascular extraembryonic membranes consists of the shell with its numerous pores and of the two fibrous shell membranes lining the inner surface of the shell, except at the air cell where they separate. In addition, at early stages of development, there may be a layer of albumen between the inner shell membrane and the vascularized yolk sac, but no quantitative data exist on the magnitude of such a layer.

The oxygen permeability of the egg shell with intact shell membranes has been measured in a number of species at different stages of incubation (Kutchai & Steen, 1971; Lomholt, 1976; Tullett & Board, 1976). Initially the permeability is low. It is in fact so low that even with the largest possible gradient in oxygen partial pressure, the oxygen requirement during the later stages of development could not be satisfied. What happens is that after about one week of incubation (chicken), the permeability of shell and membranes increases by a factor of roughly 10 to stay relatively constant for the rest of the incubation period.

The reason for the increase in oxygen permeability of the shell and membranes is to be sought in changes in water content of the shell membranes. This is high initially correlating with the finding of a low oxygen permeability. Later, the water content starts to decline quite rapidly at about the time when the permeability increase is observed. What happens is probably that the decline in water content results in the formation of more gas filled channels in the membranes which will facilitate the transport

Department of Zoophysiology, University of Aarhus, DK 8000 Aarhus C, Denmark.

of oxygen through the membranes (KUTCHAI & STEEN, 1971; LOMHOLT, 1976).

Knowing that the egg constantly loses water through evaporation, one might think of this as the reason for the dehydration of the shell membranes. The loss of water vapour from the egg is, however, constant throughout the period of incubation, whereas dehydration of the shell membranes is not. In addition, the dehydration of the membranes and the accompanying permeability increase is largely (although maybe not completely) independent of the humidity around the eggs over a large range of relative humidities (LOMHOLT, 1976). On the contrary, the reason for the change in hydration of the membranes should be sought in the conditions inside the egg. The water contained within the shell membranes must be in equilibrium with the water in the egg contents in contact with the membranes, that is at these early stages of development primarily with the albumen. At the same time the membranes start to lose water, a substantial increase in the colloid osmotic pressure of the egg white has been recorded (LOMHOLT, 1976). It has been shown that differences in protein concentration between the two sides of an excised piece of the compound shell membrane causes an osmotic flow of water, whereas a difference in salt concentration does not. Since the membranes do constitute an osmotic barrier with respect to the egg white protein, a rise in colloid osmotic pressure of the egg white will tend to draw water from the membranes.

The next factor of importance when considering the diffusive gas exchange of the embryo is the area through which diffusion takes place. The area of the shell surface of course sets an upper limit to the area available to respiratory gas exchange. It should, however, be kept in mind that during the early stages of development only a part of the shell is in contact with the extraembryonic blood vessels. In the chicken, the blood circulation is established during the second day of development (ROMANOFF, 1960). Extraembryonic blood vessels of the yolk sac are rapidly spreading over the surface of the yolk and at the same time a large amount of water is transferred from the albumen into the yolk resulting in the formation of a liquid yolk termed the subgerminal fluid beneath the embryo. This movement of water leads to a concentration of the albumen resulting in the mentioned rise in colloid osmotic pressure. Because the subgerminal fluid has a lower specific weight than the rest of the egg contents, it forces the yolk upwards bringing the yolk sac blood vessels in close contact with the inner surface of the upper part of the shell (NEW, 1956). This close contact must be important if these vessels are to function in gas exchange. It would seem that only the part of the shell in contact with blood vessels plays a role in gas exchange. A simple experiment shows this. Although turning eggs is important, they can develop without. In order to test the importance of different parts of the shell in gas exchange, some eggs had the upper half

TABLE 1: Effect of covering different parts of the egg shell on development during the first 4 days of incubation in the domestic chicken.

Part of shell covered	No. of eggs	Infertile	Died between day 2—4	Alive at day 4
No	10	0	2	8
Lower half	15	5	1	9
Upper half	15	2	10	3
All	10	0	10	0

of the shell laquered and some had the lower part laquered. For comparison some eggs were completely laquered and some were not laquered at all. The eggs were not turned.

When examined after 4 days of incubation most of the eggs with the top part of the shell laquered had died as had those with the entire shell covered, whereas those with the lower part covered had developed as well as had those not covered at all (Table 1). This is not surprising since diffusion as a means of transport is only effective over very short distances. It should be noted in this connection that the oxygen tension of albumen and yolk from completely covered eggs was not particularly low, that is the embryo is not able to deplete the entire egg contents of its oxygen, again attesting to the ineffectiveness of diffusive transport over long distances.

At the stage of development under consideration (3—5 days in chicken) the yolk is free to move with the result that in spite of turning the eggs, the embryo will always be facing upwards. If the view is accepted that gas exchange takes place primarily across the part of the shell in contact with the yolk sac vessels, a question arises as to the gas exchange during natural incubation. During the reproductive period most birds develop a brood patch, that is an area of the ventral skin which becomes defeathered and somewhat edematous (Drent, 1975). This is interpreted as a means of obtaining a close contact with the eggs thus facilitating heat transfer from the sitting bird to the eggs. This would seem to prevent a part of the shell surface from taking part in gas exchange.

The oxygen tension which can be measured on the surface of normal human skin has been reported to be only a few mm Hg at most (Evans & Naylor, 1967). It has been shown, however, that a local increase in blood flow caused by heating the skin results in a rise in skin surface oxygen tension to values close to arterial oxygen tension (Huch et al., 1973). It is tempting to speculate that a high surface oxygen tension might exist in the presumably intensely perfused brood patch.

A few preliminary attempts to record surface oxygen tension on the brood patch of the Chicken and the Budgerigar, however, showed values of only a few mm Hg. This was done on hand-held birds and since the blood flow to the brood patch is probably under acute control, the possibility of a high surface oxygen tension cannot be completely ruled out before it is possible to record from undisturbed birds. Speaking against the possibility of a high surface oxygen tension is the histological finding that the stratum corneum of the brood patch is more strongly developed during the reproductive period (Drent, 1975).

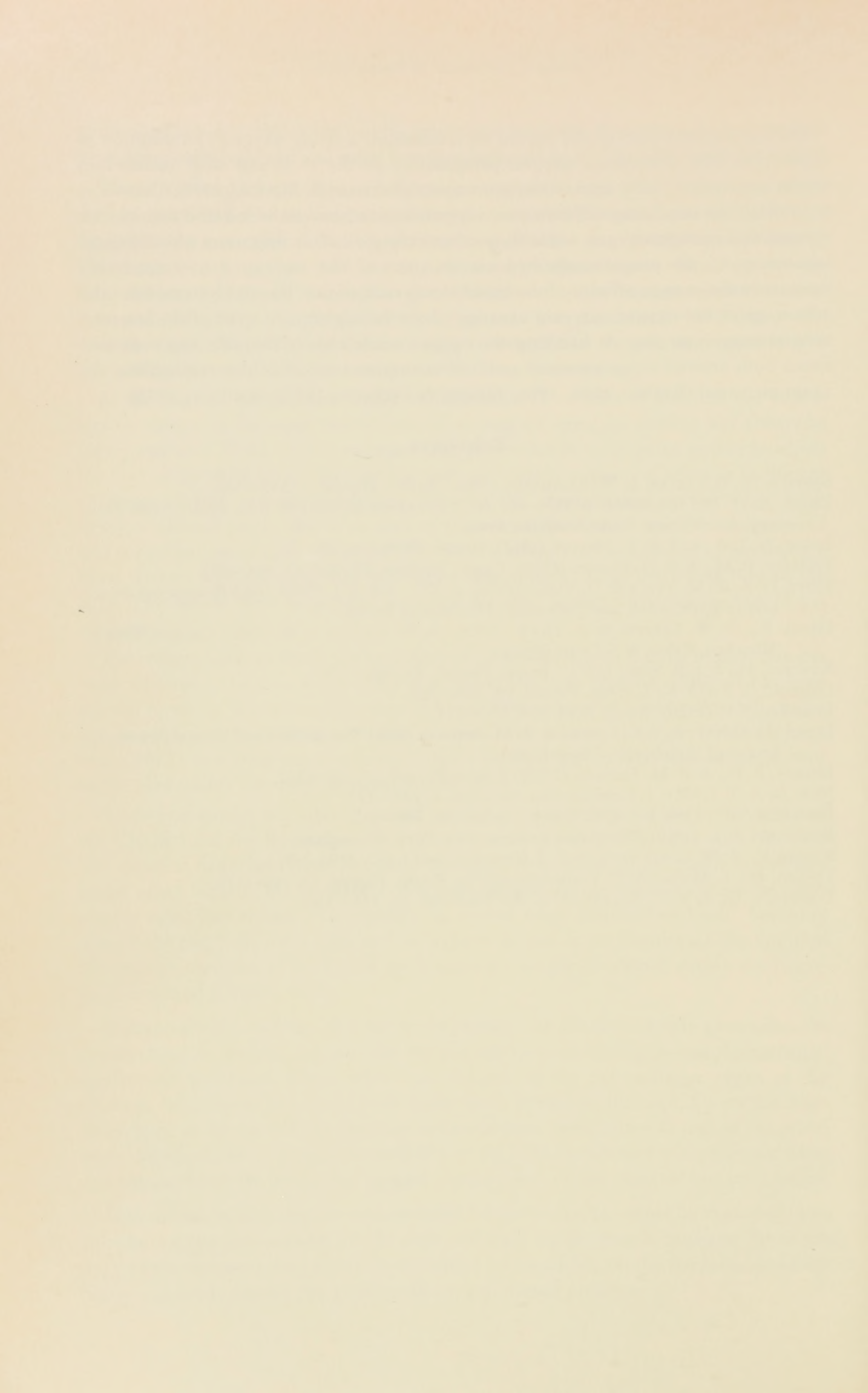
Between the 6th and the 10th day in the chicken the allantois rapidly grows into the extraembryonic coelom. It fuses with the chorion to form the highly vascularized chorioallantoic membrane which takes over the role as the gas exchange organ of the embryo, covering by day 10—11 the entire inner surface of the shell. Up to this stage an increase in the area of the vascular extraembryonic membranes as well as the previously discussed rise in oxygen permeability of the shell membranes are important when considering how the increasing oxygen consumption of the embryo can be satisfied.

After about the 10th day the area available for gas exchange cannot be expanded more and the oxygen permeability of the shell and shell membranes is constant. From this stage of development the embryo must depend on expanding on the last term in the diffusion equation, namely the gradient in oxygen partial pressure.

During the later part of the period of incubation, a rising oxygen consumption in connection with a constant oxygen permeability of the shell and shell membranes results in a decline in the arterial oxygen tension (FREEMAN & MISSON, 1970; TAZAWA et al., 1971). The increasing difference in oxygen tension between blood and ambient air ensures that enough oxygen will diffuse across the shell. One important physiological adjustment to the progressively hypoxic situation of the embryo is a concomitant increase in the oxygen affinity of the blood. As a result of this, the embryo can still take advantage of the oxygen carrying capacity of the hemoglobin in spite of the lowered arterial oxygen tension. At hatching the oxygen availability is abruptly improved and hence both arterial oxygen tension and half saturation tension of the hemoglobin are again increased (BARTELS et al., 1966; MISSON & FREEMAN, 1972; LOMHOLT, 1975).

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SYMPOSIUM ON FLIGHT AERODYNAMICS AND ENERGETICS

5. VI. 1978

CONVENERS: W. NACHTIGALL AND H. OEHME

Bird Flight: Kinematics of Wing Movement and Aspects of Aerodynamics

WERNER NACHTIGALL

Kinematics of wing movements during flapping fligth

The kinematical conditions and their relation to aerodynamics based on the most precise analysis of a wing beat available to date will be described for a downstroke period. Data were measured by my coworker DIETRICH BILO (1971). For aerodynamical reasons, a geometrical twisting (increasing proportion from base to tip) of the bird's wing must occur during downstroke. From a biological point of view, it would be useful if the degree of twisting could be correlated to the momentary speed of wing beating and flight in the sense of a variable pitch propeller. The question now arises: Is a bird's wing really analogous to a variable pitch propeller?

Proof of geometrical wing twisting

To answer this question, one must produce proof by means of technical measurements, that the wing is really twisted. Fig. 1 confirms this. Here the upper surface of ten different profile cuts (n = 0, basal cut nearest to the wing joint; n = 0, distal cut within the region of free feathers) of the right wing of a house sparrow flying freely in a wind tunnel are displayed. The wing has been photographed half way through the downstroke at approximately maximum stretching.

Photogrammetrical analysis shows (Fig. 1) that the geometrical angle of attack increases from base to tip from −3.9° to +20.1°. The geometrical angle of attack is defined by the angle between the chord line (broken line) observed and the x—y plane of a wing fixed system of coordinates. The latter begins at the proximal end of the front edge of the wing (point 55) and rotates with the beating wing. Fig. 2.1 shows the phase photograph which was used to analyse the beat position of Fig. 1 with points of measurement marked.

Proof that the geometrical wing-twisting alters according to the speed of beating

The next thing to be shown is that the above mentioned parameters alter similarly to a variable pitch propeller when the conditions of speed change.

Measurements show this to be true. During downstroke the geometrical angle of attack α_{geom} of each wing section n alters in a characteristic way (Fig. 2.2: functions α_{geom} (t); parameter n. The downstroke begins with picture 30 and ends with 46. The distance between two pictures is 1.92 milliseconds). The downward beating wing alters the direction regularly. This is shown in Fig. 3.1 with the angle of beating φ plotted as a function of the angle of forward movement ϑ. The solid, dashed and dotted curves represent the hand joint, the finger tip and wing tip respectively. The numbers represent the time (picture numbers); compare Fig. 2.2. The angle of beating φ is an index for the downward movement, the angle ϑ for the forward movement of the wings (see BILO, 1972, for exact definitions). It follows, that the wings beat downwards and then

Zoologisches Institut der Universität des Saarlandes, 6600 Saarbrücken, Bundesrepublik Deutschland

more strongly forwards during the last third of a beating period. The distance between the two picture numbers gives the speed. It can be seen from Fig. 2.2 that the geometrical angle of attack in the primaries becomes increasingly negative until $t = 37$ (pronation). Fig. 3.1 shows that the vertical component of speed of the hand joint increases up to this point. Therefore the increase in pronation of the primaries is coupled with higher speeds.

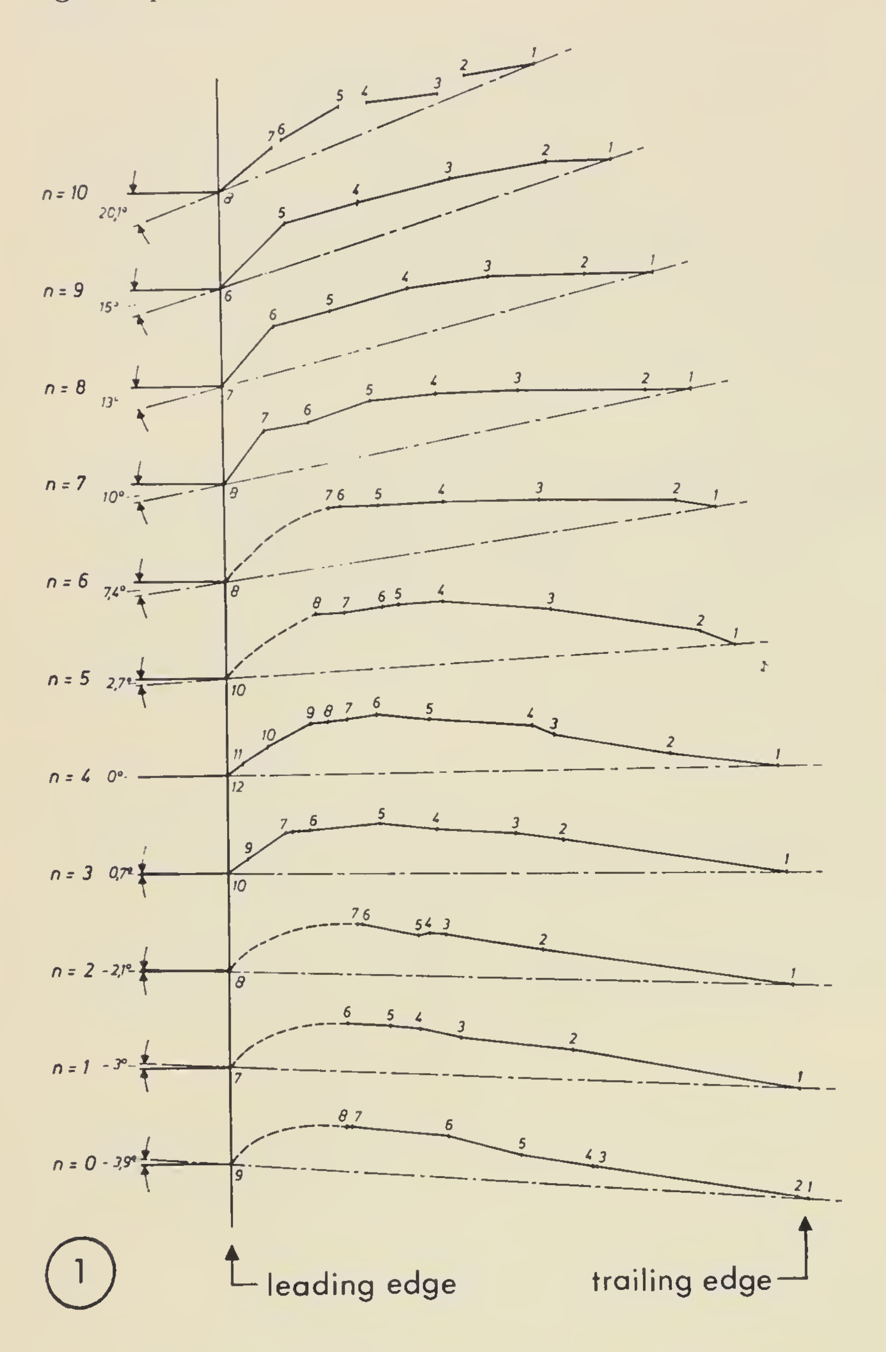


FIGURE 1. Curvature and geometrical angle of attack of a house sparrow's wing which crosses frontal plane during downstroke (see Fig. 2.1). The wing is divided in 10 profile cuts (No 0 at wing base, No 10 near wing tip). (Figs. 1 to 3.3 after BILO 1971)

Beyond $t = 37$ the primaries supinate abruptly: the geometrical angles of attack become increasingly positive. Following Fig. 4, the vertical beating movement of the hand joint brakes abruptly at $t = 37$. From this point onwards, the hand joint is pulled forwards and downwards at a decreasing speed till $t = 44$. Therefore decreasing pronation is coupled with decreasing speed which confirms what I wanted to prove.

Proof of an aerodynamical advantage of the direction of twisting

The question now arises whether the geometrical twisting and the direction of its alterations are useful, i.e. do they have an aerodynamical advantage? Fig. 3.2 shows that this is the case. The aerodynamical angle of attack α_a is given here as a function of

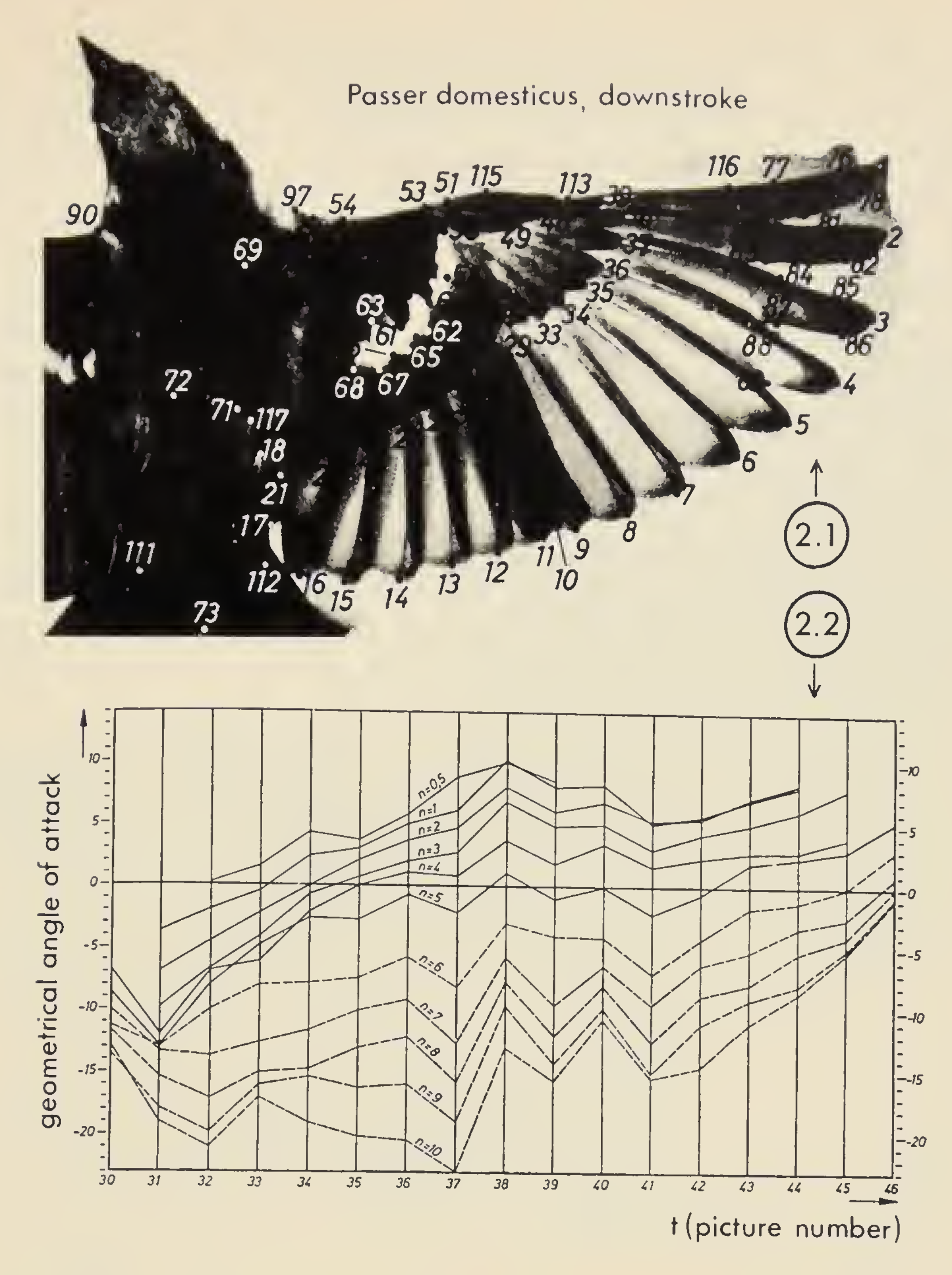


FIGURE 2.1. A house sparrow's wing in position analysed in Fig. 1

FIGURE 2.2. Geometrical angle of attack (see Fig. 1) of profile cuts 1 to 10 as a function of time. Abscissa: No 30 start, No 46 end of downstroke

the profile number n and the time t. Each curve in the α_a diagram represents one angle of attack and shows the distance n to the shoulder joint at which this angle of attack occurs during a downstroke at various successive points in the time. The numbers given at the single curves represent the α_a values in degrees; solid lines show positive angles of attack, dashed lines, negative angles of attack. The angle between the chord line and the speed of wind is defined as the aerodynamical angle of attack.

Two important results are shown by Fig. 3.2 Firstly, the aerodynamical angle of attack is almost always positive, as we expected. Only at the beginning of beating (left) is the wing interior (below) with $\alpha_a = -5°$ slightly negative for a short period (left below).

Secondly, values within the aerodynamically useful region lie between small and medium angles of attack, up to about $+20°$. Only the wing tip (top) reaches, towards

the end of the downstroke (right), higher values of about 30° (right top).

This very important result shows that strong twisting is aerodynamically positive. Over the entire wing and during the whole downstroke, small to medium aerodynamically useful, positive angles of attack are achieved.

Proof of a periodical change in camber

The twisted wing changes its geometrical angles of attack from base to tip regularly like a propeller blade and induces useful aerodynamical angles of attack over the whole surface. Like a variable pitch propeller, the bird's wing alters the angles of attack regularly and functionally with the speed. In another point, the wing is even better than its technical counterpart; it can alter its camber during the beating period.

Fig. 3.3 shows the change in profile at n = 7 as a function of time. At the beginning of downstroke (picture number 30) the profile is rather flat, which is also the case towards the end of the downstroke (picture number 46). However, between these periods the wing drastically alters its curvature.

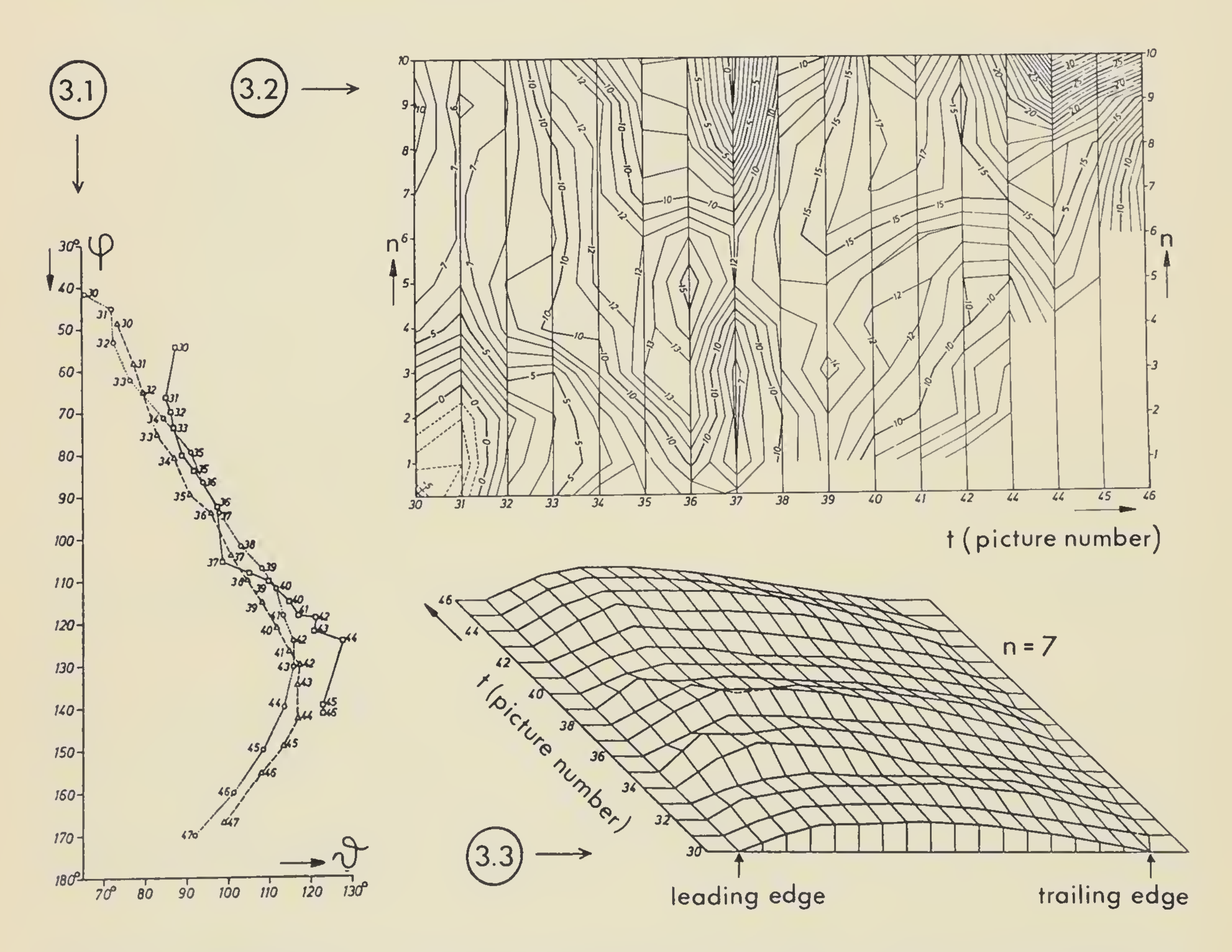


FIGURE 3.1. Downward (φ) — forward (ϑ) movement of a sparrow's wing. For explanation see text

FIGURE 3.2. Aerodynamic angle of attack of profile cuts 1 to 10 (see legend Fig. 1) during downstroke (see legend Fig. 2.2)

FIGURE 3.3. Change in camber of upper curvature of profile cut No 7 during downstroke (see legend Fig. 2.2)

Some aspects of aerodynamics

Influence of the REYNOLDS number

A pigeon with wing depth $l = 0.1$ m, flying at $v = 10$ m s^{-1}, has the REYNOLDS number $Re = v\,l\,\nu^{-1} = 10$ m $s^{-1} \cdot 10^{-1}$ m $\cdot 15^{-1} \cdot 10^{6}$ m^2 $s^{-1} = 6.7 \cdot 10^4$. A small aeroplane with $l = 1$ m, flying at 180 km h^{-1} ($v = 50$ m s^{-1}), has the REYNOLDS number $Re = 3.4 \cdot 10^6$. A general rule is, that geometrically similar conditions of flow, and therefore an aerodynamic comparison of two objects, are only possible at (approximately) similar REYNOLDS numbers. Therefore, aeroplanes and birds cannot be directly compared. However, it is possible to compare wing models or model aeroplanes and birds, since they lie within the same REYNOLDS number range. This range is also characterized by the fact, that the aerodynamic force coefficients as functions of the flight speed can drastically alter: this is the influence of REYNOLDS number.

If one raises the wind speed and thus the REYNOLDS number during wind tunnel experiments, the drag coefficient of a rounded body will sink drastically after reaching a certain critical REYNOLDS number. The previously laminar flow of the boundary layer stalls at the widest parts of the body and creates strong eddies. After exceeding the critical Reynolds number, the boundary layer flow is turbulent. This means, it is richer in energy and thus in a better condition to compensate the increase in pressure behind the widest part. It also remains attached longer to the ball and developes less drag, because it stalls at a smaller area of separation ("PRANDTL's ball test"). The range $Re < Re_{crit}$ is known as the "undercritical range", the higher one $Re > Re_{crit}$ as the "overcritical range". All rounded bodies and most certainly all birds' bodies show a behaviour similar to that of the ball tested by PRANDTL.

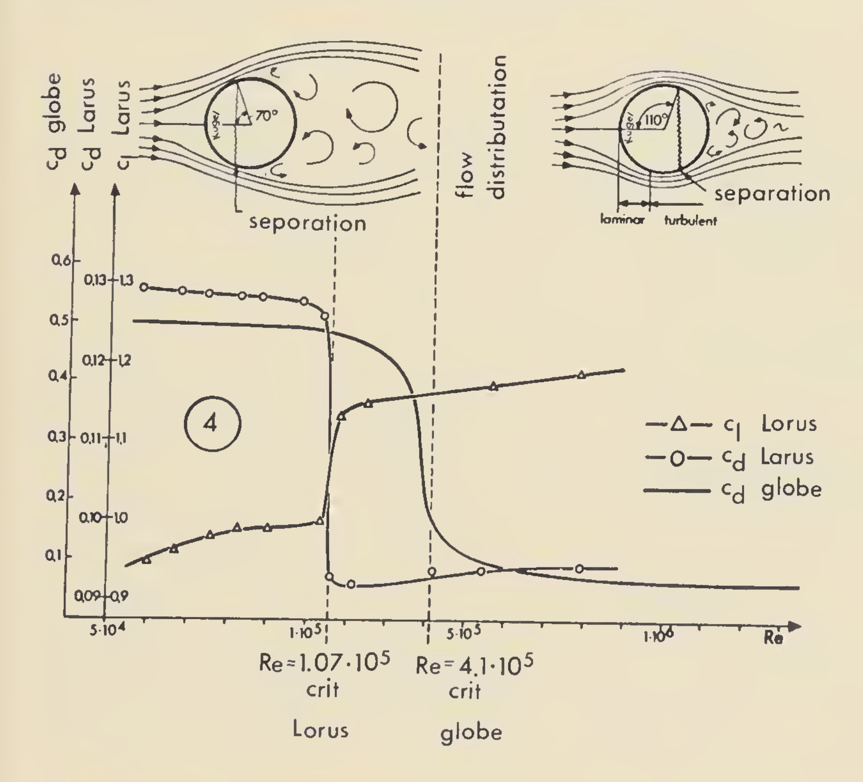
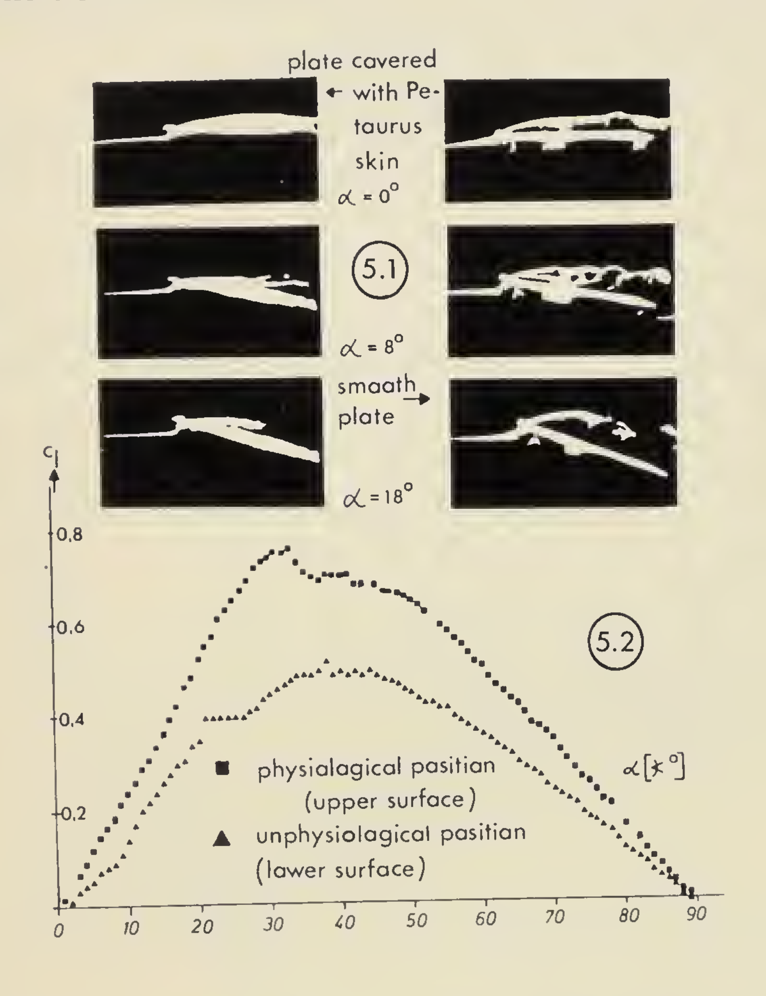


FIGURE 4. Lift (c_l) and drag (c_d) coefficients of a plaster model of *Larus ridibundus* and of a globe dependent on Reynolds number Re (After FELDMANN 1944)

So far, this behaviour has only been measured on technical, smooth models of birds. Fig. 4 shows the function c_d (Re) measured at $\alpha = 5.1°$ according to measurements made by FELDMANN (1944) on a smooth plaster of Paris model of *Larus ridibundus* (body and wings in gliding position). Re_{crit} lies at $1.07 \cdot 10^5$. The supplementary function c_l (Re) shows the sudden improvement of lift generation after the "overcritical"

flow conditions have been reached. Under- and overcritical flow can also be established around an airfoil. A functioning airfoil of overcritical flow can reach the undercritical range of flow when the speed decreases and thus the REYNOLDS number is reduced. Thus $c_{l\,max}$ suddenly decreases and c_d increases, so that the gliding angle deteriorates drastically. Measurements made on technical profiles geometrically exactly similar to bird profiles showed that this is true for natural profile forms, too (NACHTIGALL & CLAUSSEN, in prep.).

However, if one roughens the profile, especially on the leading edge, a change in flow from laminar to turbulent, and therefore overcritical flow can be achieved already at such low Re numbers at which the smooth profile would still be in undercritical flow conditions.



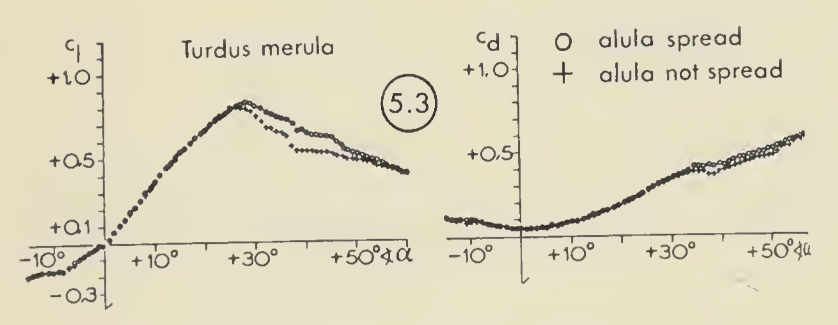


FIGURE 5.1. Smoke separation of a flat plate with and without fur cover

FIGURE 5.2. Lift polars of a flat plate, fur covered on the suction and pressure side

FIGURE 5.3. Lift polar c_l (α) and drag polar c_d (α) of a bird wing with alula spead and not spread

The fact that "biologically rough" surface areas play an important role in gliding flight is beyond doubt. Measurements made by NACHTIGALL on the outstreched skin folds of the gliding marsupial *Petaurus stellaris* show the following. As may be expected the flow on the upper side of a flat metal plate will separate already at very small angles of attack at the leading edge, as can be seen from the smoke tunnel pictures in Fig. 5.1.

If one glues the flight skin of *Petaurus,* in the right direction, to this metal plate, the flow will remain completely attached up to $\alpha \approx 6-8°$ and partly attached up to $\alpha \approx 20°$. This results in higher c_l values and a more suitable polar without the hard descent after $c_{l\,max}$ (Fig. 5.2).

Fore-wings as high lift devices

Technical fore-wings attain extremely high c_l values, up to $c_l = 2.2$ and continue to function at extremely high angles of attack, up to $\alpha = 30°$. The cause for this behaviour lies in the influence of the flow streaming through the slit on the boundary layer. Whether the spread primaries of a bird will display such an effect, as may be expected, cannot as yet be definitely decided. However, the effect of a biological "fore-wing", namely the alula, is certain. During starting, landing and flying in curves, when the danger of stalling due to too high angles of attack is acute, the alula is streched out. Lift will be improved by 10—20 % and $c_{l\,max}$ will be expanded to larger angles (NACHTIGALL & KEMPF, 1971). Greater effects are no doubt achieved by the extra large alulae of the storks and herons which must fly at high angles of attack during near hovering flight in descending to the nest. Furthermore, it may definitely be assumed that the alula plays an important role during beating and gliding flight.

Research on bird flight is still very much in progress even though certain important points have already been successfully dealt with. The same can be said of the research on energetics of bird flight (ROTHE & NACHTIGALL, 1980). Further cooperation between biologists, physicists and engineers will be necessary before the most important questions on bird flight can be solved.

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Kinematik und Energetik des Rüttelfluges mittelgroßer Vögel

Holger H. Dathe und Hans Oehme

Problemstellung

Das Standschweben als ideale Form des Rüttelfluges bei Windstille erscheint analytisch leicht zugänglich, weil das Gewicht die einzige dabei zu kompensierende Kraft ist. Hertel (1963) hat die Verhältnisse beim rüttelnden Kolibri in Analogie zum Hubschrauber mit der Annahme eines stationären Hubstrahls nachgebildet. Sein Modell ist später von Pennycuick (1968), Weis-Fogh (1972, 1973) und Norberg (1975) modifiziert bzw. auch auf andere Vögel übertragen worden. Die Ergebnisse dieser Arbeiten lassen aber auch Zweifel an der universellen Gültigkeit des einfachen Hubstrahl-Modells zu. Im Gegensatz zum Rüttelspezialisten Kolibri muß bei anderen Vögeln die Möglichkeit instationärer Verhältnisse stärker beachtet werden. So gibt es bei ihnen höchstwahrscheinlich keine kontinuierliche Krafterzeugung über den ganzen Schlagzyklus, denn in Ab- und Aufschlag ändern sich die Flügelgeometrie und die kinematischen Größen. Die Massen der wirkenden Muskeln sind sehr unterschiedlich.

Die vorliegende Studie versucht eine günstigere Annäherung an die realen Verhältnisse durch die Zerlegung des Bewegungsablaufs in Teilphasen, die jede für sich nach den Prinzipien der stationären Aerodynamik behandelt werden. Das Verfahrensprinzip wird am Beispiel zweier gemeiner Vogelarten *(Columba livia* und *Larus ridibundus)* demonstriert, und erste Ergebnisse werden mitgeteilt. Eine ausführliche Darstellung unter Einbeziehung weiterer Arten bleibt einer späteren Publikation vorbehalten.

Material und Meßwertermittlung

In die Berechnungen gingen die Durchschnittswerte aller erforderlichen morphologischen und kinematischen Daten ein. Für jede Art wurde ein „Standardvogel" ermittelt, der zumindest für die Herkunftspopulation als repräsentativ anzusehen ist. Die kinematischen Basisdaten wurden an freifliegenden Tieren ermittelt. Morphologische Daten waren: Körpermasse, Masse der Flugmuskeln (M. pectoralis/M. supracoracoideus, M. deltoideus major), Länge des gestreckten Flügels und des Handflügels, Umrißgeometrie des Flügels (Flügeltiefenverteilung).

Kinematische Daten waren: Schlagwinkel, V-Winkel, Winkelgeschwindigkeit des Flügels, Zeitmuster der Schlagphasen.

Zur Methodik vgl. auch Dathe & Oehme (1978).

Rüttelbewegung von Haustaube und Lachmöwe

Bei beiden Arten kann der Schlagzyklus in gleicher Weise in 6 Phasen unterteilt werden (Abb. 1 und 2): Abschlag und Aufschlag, die jeweils noch in einen forcierten Abschnitt (1) und einen trägheitsbedingten „Ausschwingabschnitt" (2) zu trennen sind, sowie zwei Umkehrphasen. Der Abschlag 1 wird mit gestrecktem Flügel von oben hin-

Akademie der Wissenschaften der DDR, Forschungsstelle für Wirbeltierforschung (im Tierpark Berlin), DDR-1136 Berlin, Am Tierpark 125.

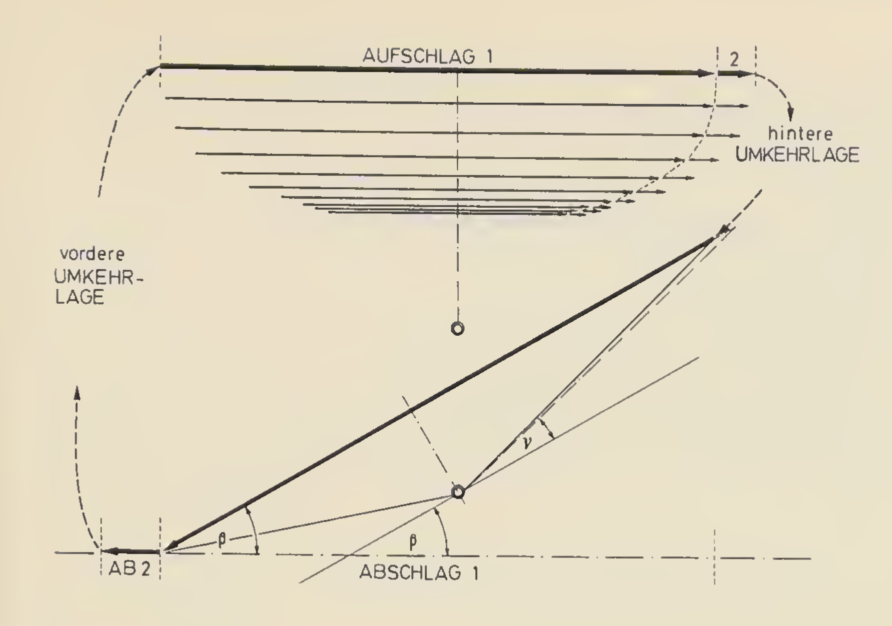


Abb. 1. Schema der Bahnkurve der Flügelspitze in Seitenprojektion (Drehpunkt vertikal versetzt). Im Aufschlag ist der Handflügel aufgefächert. Die Schlagphasen 1 sind forciert, Schlagphasen 2 passiv (Ausschwingen infolge Massenträgheit). β = Neigung der Schlagbahnebene, ν = V-Winkel des Flügels gegen die Ebene des Kegelgrundkreises.

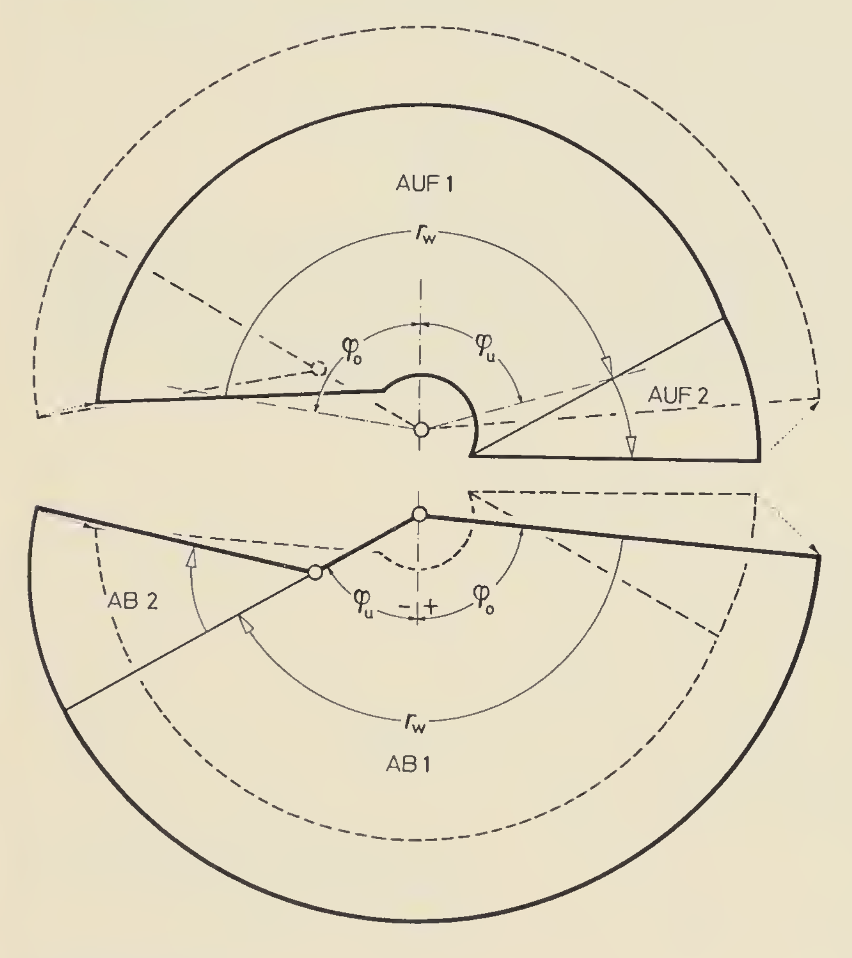


Abb. 2. Schema der Flügelbewegung in der Schlagbahnebene. Oben Aufschlag, unten Abschlag ausgeführt. r_w = Bahn des „wirksamen Radius", φ_o und φ_u = oberer bzw. unterer Flügelwinkel (nur für Ab- und Aufschlag 1 eingezeichnet).

ten auf einer um den Winkel β geneigten Schlagbahn nach vorn unten geführt. Der Flügel ist dabei um den V-Winkel ν gehoben, so daß er den Teil eines Kegelmantels überstreicht. Bis zur vorderen Endlage schwingt der Handflügel allein weiter, während der Armflügel stehenbleibt (Abschlag 2). In der vorderen Umkehrlage wird der Flügel weiter gebeugt, sehr schnell supiniert und, senkrecht gestellt, nach oben geführt. Im Aufschlag 1 wird der gebeugte Flügel bei stark gespreizten Handschwingen um das Schultergelenk zurückgedreht. Die getrennten Handschwingen wirken dabei vermutlich wie ein Mehrdecker. Am Ende der Drehung löst sich der Handteil aus der starren Verbindung mit dem Arm und schwingt passiv weiter (Aufschlag 2). In der oberen

Umkehrlage wird der Arm durchgestreckt und der Flügel in die Ausgangsposition des Abschlags gehoben. Diese Rüttelweise entspricht dem Typ 1 bei DATHE & OEHME (1978).

Prinzip des Berechnungsverfahrens

Abschätzung der Strahlgeschwindigkeit (v_k)

Im Standschweben spielt die durch den Flügel erzeugte axiale Zusatzgeschwindigkeit für die effektive Anblasgeschwindigkeit eine entscheidende Rolle. Sie wurde, getrennt für Ab- und Aufschlag, aus den jeweiligen Hubkräften F_H berechnet, wobei $\sum F_H \cdot \tau = G$.

$$v_k^2{}_{ab}(A_{k\,ab\,1}\,\tau_{ab\,1} + A_{k\,ab\,2}\,\tau_{ab\,2}) + v_k^2{}_{auf}\,(A_{k\,auf\,1}\,\tau_{auf\,1} + A_{k\,auf\,2}\,\tau_{auf\,2}) = \frac{G}{2\rho}$$

Die Strahlleistungen sollen sich auf Auf- und Abschlag verteilen wie die jeweils beteiligten Muskelmassen. Es wird vorausgesetzt, daß Abschlags- und Aufschlagsmuskeln die gleiche spezifische Leistungsfähigkeit haben.

$$\frac{P_{St\,ab\,1}}{P_{St\,auf\,1}} = \frac{A_{k\,ab\,1}\,\tau_{ab\,1} \cdot v_k^3{}_{ab}}{A_{k\,auf\,1}\,\tau_{auf\,1} \cdot v_k^3{}_{auf}} = \frac{m_{ab}}{m_{auf}}$$

v_k ist die Durchtrittsgeschwindigkeit durch die vom Flügel überstrichene Fläche. Sie soll in jedem Falle senkrecht zur Schlaggeschwindigkeit stehen (Abb. 3), muß aber mit dem V-Winkel ν korrigiert werden. Die Durchtrittsgeschwindigkeiten $v_{k\,ab}$ und $v_{k\,auf}$ wurden mit einem Suchprogramm unter den genannten Voraussetzungen ermittelt.

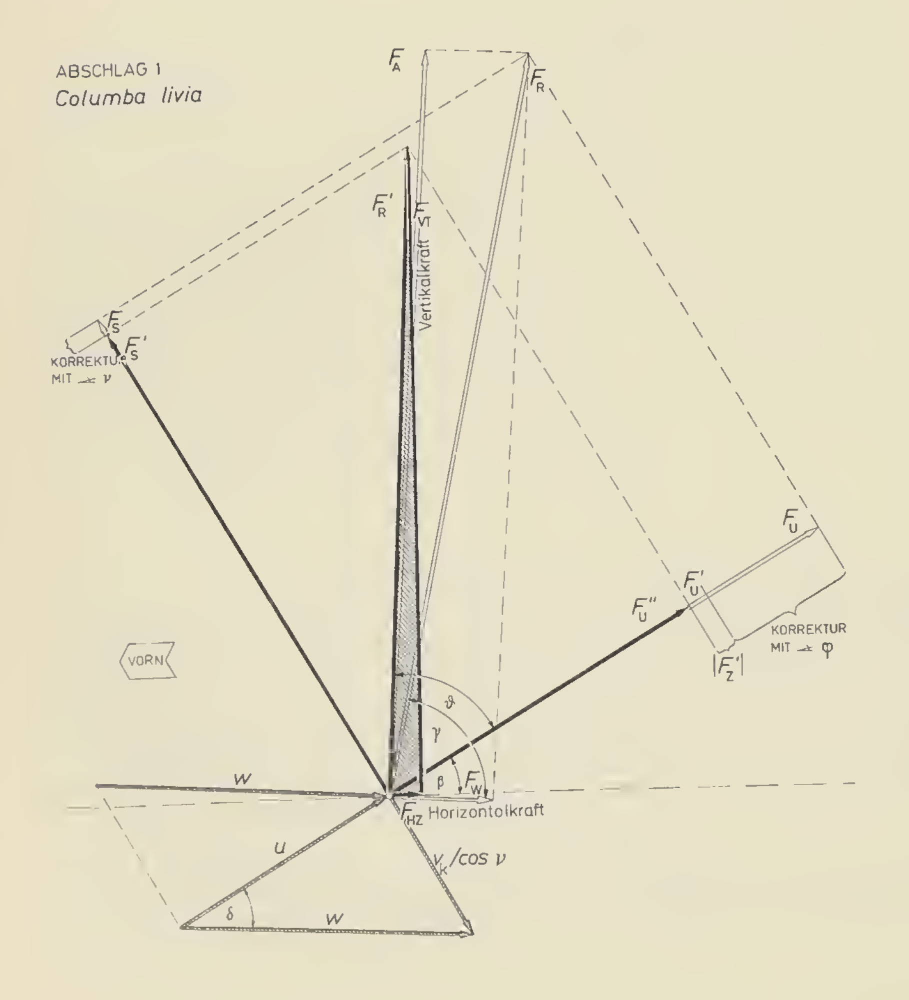


Abb. 3. Plan der Geschwindigkeiten und Kräfte am Flügelelement. Die Umfangskraft F_U ist gemäß dem Schlagwinkel φ zu korrigieren; ein V-Winkel ν beeinflußt den wirksamen Anteil der Schubkraft F_S und über eine entsprechende Zentripetalkraft F_Z auch F_U. Die Neigung der Schlagbahnebene β bestimmt entscheidend das Verhältnis zwischen Vertikal- und Horizontalkraft (F_{VT}, F_{HZ}). v_k = Durchtrittsgeschwindigkeit, u = Schlaggeschwindigkeit, w = resultierende Anblasgeschwindigkeit.

Kräfte am Flügel

Das in den Abb. 1—3 am Beispiel des Abschlages 1 der Haustaube skizzierte Prinzip gilt sinngemäß für alle Phasen des Ab- und Aufschlages bei beiden Arten. Abb. 3 veranschaulicht Kräfte und Geschwindigkeiten am Flügel.

Die resultierende Anblasgeschwindigkeit w ergibt sich aus der korrigierten Durchtrittsgeschwindigkeit $v_k/\cos\nu$ und der Schlaggeschwindigkeit $u = \omega\, r \cos\nu$ zu

$$w^2 = u^2 + v_k^2/\cos^2\nu = \omega^2 r^2 \cos^2\nu + v_k^2/\cos^2\nu .$$

Aus der Grundbeziehung $F_A = c_a A \frac{\rho}{2} w^2$ berechnet sich der Quertrieb F_A für ein Flügelelement nach

$$dF_A = c_a \frac{\rho}{2} dA \left(v_k^2/\cos^2\nu + \omega^2 r^2 \cos^2\nu\right)$$

$dA = f(r)\, dr$ (f (r) ist die Flügeltiefenverteilung)

$$dF_A = c_a \frac{\rho}{2} \left[\left(v_k^2/\cos^2\nu\right) f(r)\, dr + \omega^2 r^2 \cos^2\nu\, f(r)\, dr\right]$$

Konstantes c_a über R vorausgesetzt, gilt für den gesamten Flügel

$$F_A = c_a \frac{\rho}{2} \left[v_k^2/\cos^2\nu \int_0^R f(r)\, dr + \omega^2 \cos^2\nu \int_0^R r^2 f(r)\, dr \right]$$

Das erste Integral in der Klammer ist die Flügelfläche, das zweite ist das Flächenträgheitsmoment I des Flügels, das auch den „wirksamen Radius" r_w liefert: $r_w^2 = I/A$.

Der Flügelwiderstand wird über die Gleitzahl $\varepsilon = c_w/c_a$ eingeführt. Daraus ergeben sich

die resultierende Luftkraft $F_R = F_A \sqrt{1 + \varepsilon^2}$,

die Umfangskraft $F_U = F_R \sin(\gamma + \delta)$ und

die Schubkraft $F_S = F_R \cos(\gamma + \delta)$, wobei

$$\varepsilon = \tan\gamma, \quad v_k/\left(u_{r_w} \cos\nu\right) = \tan\delta .$$

Diese Kräfte müssen korrigiert werden, bevor sie in die Bilanz der horizontalen und vertikalen Kräfte eingehen. Durch den V-Winkel ν reduziert sich die Schubkraft parallel zur Sagittalebene auf $F_S' = F_S \cos\nu$, es entsteht aber in Richtung auf den Drehpunkt eine Schubwirkung $F_Z = F_S \sin\nu$ (Zentripetalkraft). Die mittlere wirksame F_Z beträgt parallel zur Sagittalebene

$$F_Z' = F_Z \left(\frac{1 - \cos\varphi_o}{\varphi_o} + \frac{1 - \cos\varphi_u}{\varphi_u} \right)$$

(wenn φ_o und φ_u verschiedene Vorzeichen haben; s. Abb. 2). φ_o und φ_u, die gegen die Sagittalebene gemessenen Winkel der Flügelstellung am Beginn und Ende der Schlagphase, korrigieren auch F_U (vgl. OEHME & KITZLER, 1975 p. 439):

$$F_U' = F_U \frac{\sin\varphi_o - \sin\varphi_u}{\varphi_o - \varphi_u}$$

Die schließlich wirkende mittlere Umfangskraft ist

$$F_U'' = F_U' - F_Z'$$

Die korrigierte Resultierende F_R' ergibt sich aus

$$(F_R')^2 = (F_U'')^2 + (F_S')^2,$$

ihre vertikale bzw. horizontale Komponente nach

$$F_{VT} = F_R' \sin(\beta + \vartheta) \quad \text{und}$$

$$F_{HZ} = F_R' \cos(\beta + \vartheta), \quad \text{wobei} \ \tan\vartheta = F_S'/F_U''.$$

Kräfte- und Leistungsbilanz

Für das Standschweben gilt $\sum F_{VT}\,\tau = G$ und $\sum F_{HZ}\,\tau = 0$. Dabei ist τ der Zeitanteil des Zyklusabschnittes, bezogen auf die Zyklusdauer. Bei gleicher spezifischer Leistungsfähigkeit der beteiligten Muskeln ist weiter zu fordern:

$$\frac{P_{ab\,1}\,\tau_{ab\,1}}{P_{auf\,1}\,\tau_{auf\,1}} = \frac{m_{ab}}{m_{auf}} = \frac{m_{Pect}}{m_S + m_D}$$

m_{Pect} = Masse des M. pectoralis, $m_S + m_D$ = Massen des M. supracoracoideus plus M. deltoideus major.

Die aktuelle Leistung der Schlagphase ist $P = F_U\,\omega\,r_w$.

Mit Hilfe eines Computers wurden für c_a, c_w und β Wertekombinationen gesucht, die für die gemessenen bzw. berechneten morphologischen und kinematischen Daten des Standardvogels die oben genannten Bedingungen erfüllen (Tabelle 1).

TABELLE 1. Quertriebsbeiwerte (c_a), Widerstandsbeiwerte (c_w) und Neigungswinkel der Schlagbahnebene (β) im Ergebnis der Kräfteausgleichsrechnung

	Abschlag		Aufschlag		Abschlag 1
	c_a	c_w	c_a	c_w	β
Haustaube	2,8	0,42	0,5	0,12	30,3°
Lachmöwe	2,1	0,26	0,2	0,06	33,2°

Diskussion

Die Quertriebsbeiwerte des Abschlags fallen sehr hoch aus. Bei technischem Fluggerät wären dafür Hochauftriebsmittel erforderlich; Vogelflügel sollten auf überhaupt erreichbare maximale c_a-Werte hin experimentell untersucht werden. Die Widerstandsbeiwerte sind demgegenüber möglicherweise etwas zu niedrig, im ganzen aber dürfte ihre Größenordnung zutreffen. Gemessene Werte für β streuen, sind aber etwas kleiner als die berechneten. Hier kann ein leichter Wind $< 0,5$ m/s von Einfluß sein. Die Verstellung der Schlagbahnebene ist offenbar für den Vogel eine empfindliche Steuerungsmöglichkeit bei sonst wenig variablen Bewegungsparametern.

Tab. 2 und Abb. 4 zeigen die Rüttelleistungen und ihren Zusammenhang mit den Leistungen im Streckenflug (Flugleistungen nach OEHME et al., 1977). Die Leistungen des Standschwebens liegen durchgängig über den maximalen Dauerleistungen. In ihrer absoluten Größe unterstützen sie nachdrücklich die Vermutung, daß diese Vögel beim Flug auf der Stelle tatsächlich bis an die Grenze ihres Leistungsvermögens gehen müssen. Die ermittelten Werte bewegen sich dabei im Bereich der von Vögeln bekannten Muskelleistungen. Durch Extrapolation der Rüttelleistung auf die rechte Teilparabel der Abb. 4 ergeben sich folgende Höchstgeschwindigkeiten:

Haustaube 21,3 m/s ≈ 77 km/h
Lachmöwe 17,7 m/s ≈ 64 km/h

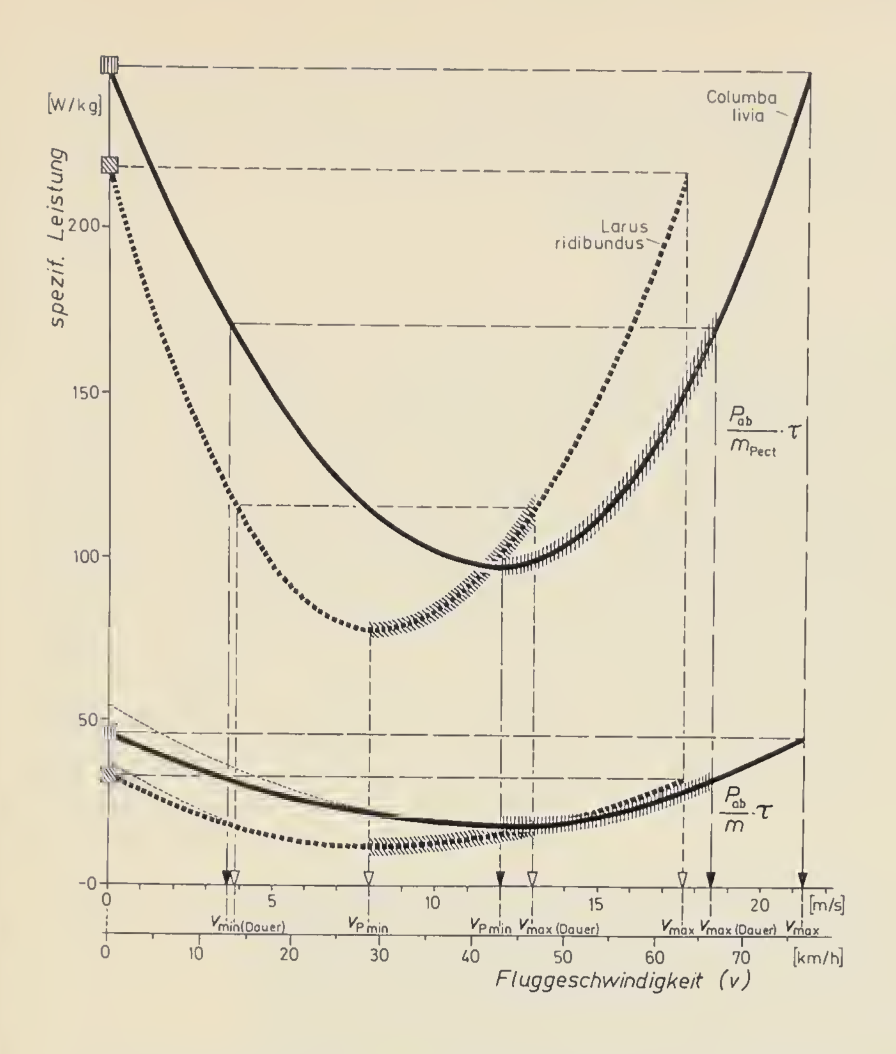


Abb. 4. Spezifische Leistung in Abhängigkeit von der Fluggeschwindigkeit bei Haustaube und Lachmöwe. Abschlagsleistung oben bezogen auf die Masse des M. pectoralis, unten bezogen auf die Körpermasse. Die schraffierten Kurvenbereiche zwischen $v_{P\,min}$ und $v_{max\,(Dauer)}$ sind experimentell ermittelt (OEHME et al., 1977), ebenso nun die Rüttelleistung; dazwischenliegende Werte sind durch Parabeln 2. Grades angenähert. Unter der Voraussetzung, daß die Rüttelleistung die höchstmögliche ist, ergibt sich die Höchstgeschwindigkeit durch Extrapolation auf die rechte Teilparabel.

Zumindest die Haustaube, von der man steile Steigflüge kennt, scheint noch über einige Reserven zu verfügen, die auch eine noch höhere v_{max} erlauben könnten. Die Ergebnisse sind aber für sich und in ihrer Relation glaubhaft und können für den Vergleich beider Arten als erste Näherung gelten. Nachfolgende Untersuchungen wären notwendig zur Ergänzung des Leistungs-Geschwindigkeitsdiagramms in den hypothetischen Bereichen. In den bisherigen Analysen wurde auch die zusätzliche Leistung bei der Beschleunigung des Flügels am Beginn der Schlagphasen und ihr Einfluß auf die Gesamtleistung noch nicht berücksichtigt. Das hier erprobte Modell dürfte aber auch dafür geeignete Ansatzpunkte bieten.

TABELLE 2. Spezifische Leistungen von Haustaube und Lachmöwe im Rüttelflug

	$\frac{P_{ab}\,\tau}{m}$ [W/kg]	$\frac{(P_{ab} + P_{auf})\,\tau}{m}$ [W/kg]	$\frac{P_{ab}\,\tau}{m_{Pect}}$ [W/kg]	$\frac{P_{rütt}}{P_{min}}$	$\frac{P_{rütt}}{P_{max\,(Dauer)}}$
Haustaube	45,94	54,26	247,87	2,52	1,45
Lachmöwe	33,37	37,29	218,24	2,78	1,88

Summary

Calculation of forces and power of hovering flight in *Columba livia* and *Larus ridibundus* was performed by dividing the wing beat cycle into phases defined by kinematical and geometrical data of the wing, the phases themselves being treated on principles of steady aerodynamics. Average values from morphological measurements and from analyses of slow motion films were used

for a "typical bird" of the species concerned. Aerodynamic coefficients of the wing were determined on the conditions of equilibrium of forces and the given ratio power of downstroke/power of upstroke (≙ ratio of masses of the acting flight muscles). Results coincide with aerodynamic knowledge and give rise to statements on avian flight capacity.

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The Aerodynamic Characteristics of Slotted Wing-tips in Soaring Birds

DIETRICH HUMMEL

Introduction

In gliding flight a large number of medium and large-sized birds, such as for instance crows (Corvidae), hawks (Accipitridae), storks (Ciconiidae), cranes (Gruidae), pelicans (Pelecanidae), pheasants (Phasianidae) and bustards (Otididae), show distinctly split wing-tips. The wings of birds of these families have a relatively short span, large chord and thus a small aspect ratio. On the other hand swallows (Hirundinidae), swifts (Apodidae) and all seabirds, such as for instance albatrosses (Diomedeidae), gannets (Sulidae), fulmars and shearwaters (Procellariidae) and gulls (Laridae), have high aspect ratio wings with pointed wing-tips which are not split. In flapping flight an even larger number of bird families shows split wing-tips in certain periods of the flapping cycle, but this complicated flight condition (BILO, 1971, 1972; HUMMEL & MÖLLENSTÄDT, 1977) will not be investigated here.



FIGURE 1. Winglets at the wing-tip of a Marabou *(Leptoptilus crumeniferus)* in gliding flight, after a photo by G. RÜPPELL. Notice that the wing-plan is slotted, the winglets are staggered in height, the two uppermost and leading winglets are twisted.

The geometric shape of slotted wing-tips has been described comprehensively by GRAHAM (1932). Recent quantitative additions are due to OEHME (1977). The wing consists of an entire inner part and of the tip region divided into several winglets. The wing plan is therefore split up. The winglets are bent upwards and forwards by aerodynamic forces and some of them, especially those near the wing's leading edge, are twisted in such a way that their geometrical angle of incidence increases in distal direction. A certain geometric detail, however, has been overlooked so far and has to be added here, namely that the bent up winglets are staggered in height as shown in Fig. 1.

Institut für Strömungsmechanik der Technischen Hochschule, 3300 Braunschweig, Bundesrepublik Deutschland

Existing explanations

For the explanation of the aerodynamic function of slotted wing-tips a direct comparison with technical solutions is not possible, since slotted wing-tips are not used for wings of aircraft. Nevertheless some details of slotted wing-tips have been put into relation to devices of man-made wings and this led to certain explanations of the meaning of slotted wing-tips. The most important of them are:

Slotted wing-tips look like a multi-airfoil system which has been proposed by HANDLEY PAGE (1921) and BETZ (1922) and others to increase the maximum lift coefficient of two-dimensional airfoils. In order to get this effect, however, the small airfoils must lie very close together. In bird wings this is only true for the Alula spuria which works as a high lift device as described by GRAHAM (1932) and later by NACHTIGALL & KEMPF (1971). But the slotted wing-tips might not work as a high-lift device for two main reasons: Firstly, the distance between the winglets is too large, especially at their tips, in order to obtain a multi-airfoil effect. Secondly, in unswept wings with rounded wing-tips at high angles of attack, flow separation starts at the highly loaded inner parts of the wing. Therefore high-lift devices should be arranged there rather than in the lesser loaded outer parts of the wing, where the local lift coefficient tends to zero at the wing-tip.

Slotted wing-tips might be a device to reduce the drag of the wing. This explanation has also been proposed originally by GRAHAM (1932) and has been supported later by HERTEL (1963) and OEHME (1977). The drag D of a wing consists of the drag due to friction D_f at the wing surface and of the induced drag D_i which is due to the finite span of the wing and which depends for a given plane on the spanwise distribution of local lift:

$$D = D_f + D_i. \qquad \text{equ. (1)}$$

Slitting the wing-tips leads to an increase of friction drag D_f, since the number of leading-edges is increased in the tip-region, and the contribution of the neighbourhood of a leading-edge to the drag is larger than that of more rearward located parts of a surface, see e.g. SCHLICHTING & TRUCKENBRODT (1967/69). For a plane wing of given lift L and span b MUNK (1919) has shown that a minimum of induced drag

$$D_{im} = \frac{L^2}{\pi q b^2} \qquad \text{equ. (2)}$$

($q = \rho V^2/2$, ρ density of the air, V flight speed) exists. All wings can fly and do fly very close to this optimum by means of a proper combination of plane shape and spanwise distribution of twisting angle. Therefore, splitting the wing-tips into an arrangement of tandem winglets situated in the plane of the main wing cannot lead to a reduction of induced drag below the value according to equ. (2). This has been proved by NEWMAN (1958) and the calculations presented by OEHME (1977) are in contradiction to these principles of aerodynamics.

However, the induced drag of a wing can be reduced below the value of equ. (2) by means of staggering the lifting system in height. Such a non-planar lifting system has been used, for instance, in biplanes. The effect has been described by PRANDTL (1923). The possible drag reductions are moderate. In modern aircraft this possibility of reduction of induced drag is no longer used, because the same effect can be achieved by a slight enlargement of the wing span, see equ. (2). The wing span of birds having slotted

wing-tips is probably limited for non-aerodynamic reasons. In this case staggering of the lifting system in height in the wing-tip region seems to be an ultimate means to reduce the induced drag to its lowest possible value. This effect will be discussed by means of aerodynamic theory and by wind-tunnel experiments.

Aerodynamic theory

The aerodynamic characteristics of wings with slotted wing-tips have been investigated by means of aerodynamic theory. The calculations have been performed using a numerical panel method such as, for instance, described by KRAUS & SACHER (1973).

In Fig. 2 a typical example is shown for the drag characteristic of a rectangular wing of aspect ratio $A = 4s^2/S = 4$ (s = semi-span, S = wing area), the wing-tips of which are split at a slitting ratio $\eta_o = y_o/s$ into n winglets of equal chord-length. Firstly for all plane configurations ($\delta_{l,t} = 0$) with arbitrary values for n and η_o including the limiting cases of n tandem winglets ($\eta_o = 0$), the induced drag D_i is larger than the minimum value D_{im} according to equ. (2). The ratio D_i/D_{im} is close to unity and depends slightly on the number of winglets n and on the slitting ratio η_o. Another plane-effect, which is not shown here, is the considerable rearward shift of the local aerodynamic center in the slotted tip-region of the wing, which leads to an increase in longitudinal stability. This is a first effect of slotted wing-tips, which might be used by birds.

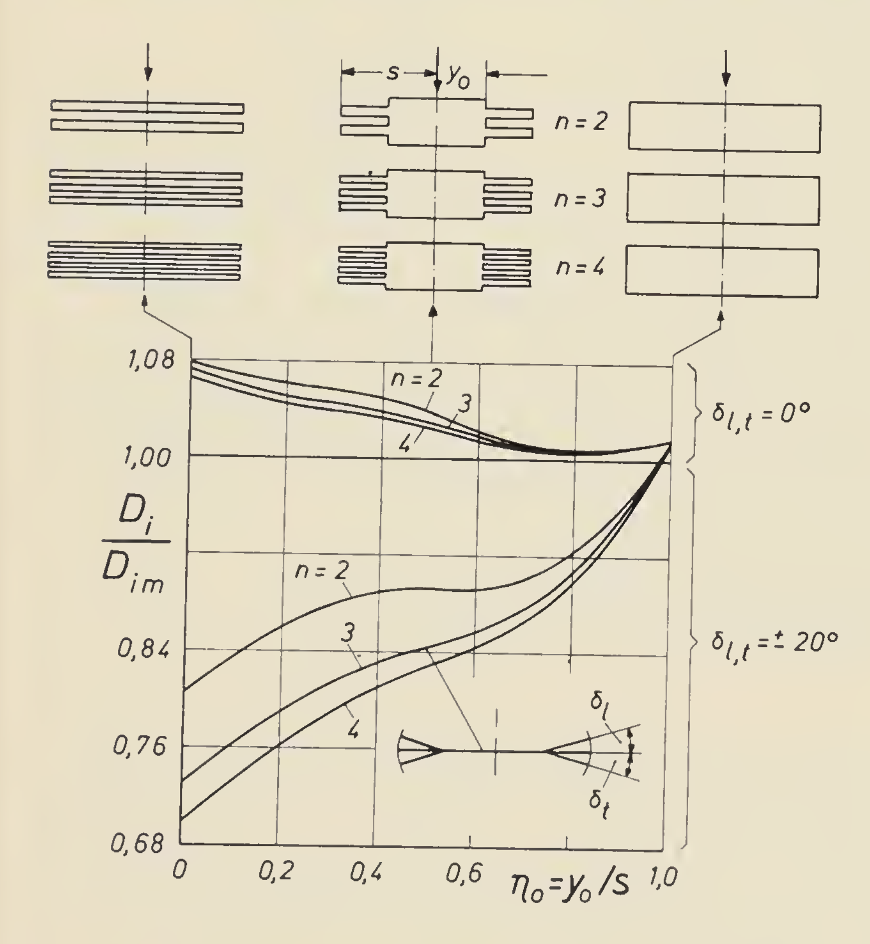


FIGURE 2. Theoretical induced drag characteristics of wings with slotted wing-tips for planar ($\delta_{l,t} = 0°$) and non-planar ($\delta_{l,t} = \pm 20°$) configurations (n = number of winglets, $\eta_o = y_o/s$ = slitting ratio, $A = 4s^2/S = 4.0$ = aspect ratio of outer rectangular wing).

Fig. 2 indicates the results for non-planar lifting systems. In these calculations, the leading winglet was set at $\delta_l = +20°$ and the trailing winglet at $\delta_t = -20°$. For $n > 2$ winglets the angle $\Delta\delta = \delta_l - \delta_t$ has been divided into equal parts $\Delta\delta/(n-1)$. The results indicate a reduction of induced drag which increases with decreasing slitting ratio η_o as well as with increasing number of winglets n. If the stagger angle δ is increased, the

induced drag reaches a minimum, which depends on the number of winglets and on the slitting ratio. For $n=3$ and $\eta_o=0.7$ its value is $D_i/D_{i\,m}=0.86$ at $\delta_{l,\,t}=\pm 35°$. This is a second effect of slotted wing-tips. The possible drag reduction is moderate.

Another result of these calculations, which is not shown here, are very large local lift coefficients which occur in the basal region of the winglets located close to the wing leading edge. Flow separations at these winglets would reduce the benefit of drag reduction. Therefore the winglets should be pointed as well as twisted in such a way that their geometric angle of incidence decreases proximally. These details are observed in wings of birds, see Fig. 1. It turns out that the drag reduction may only be achieved by a proper arrangement of the winglets.

Experimental investigations

Measurements have been carried out in the 1.3 m wind-tunnel of the Institut für Strömungsmechanik at the Technische Universität Braunschweig. Some results are shown in Fig. 3.

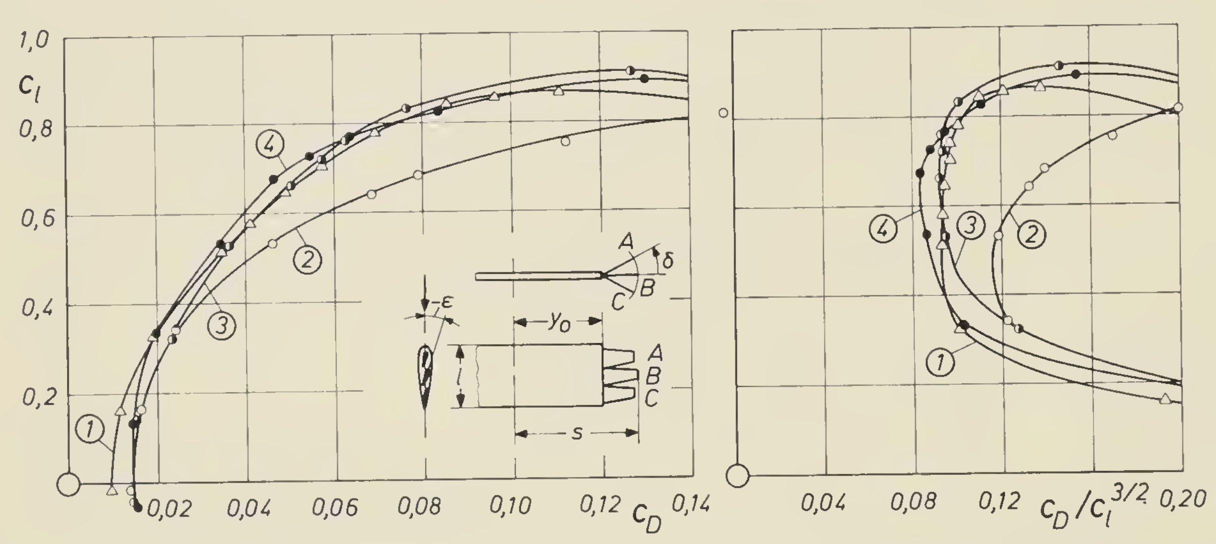


FIGURE 3. Experimental lift-drag-characteristics of wings with slotted wing-tips for planar ($\delta_{A,B,C}=0°/0°/0°$) and non-planar ($\delta_{A,B,C}=+20°/0°/-20°$) configurations. (Number of winglets $n=3$, slitting ratio $\eta_o=y_o/s=0.714$, aspect ratio of outer rectangular wing $A=4.0$).
① △ Rectangular wing, $A=4.0$
② ○ Slotted tips; $\delta_{A,B,C}=0°/0°/0°$; $\varepsilon_{A,B,C}=0°/0°/0°$
③ ○ Slotted tips; $\delta_{A,B,C}=0°/0°/0°$; $\varepsilon_{A,B,C}=-10°/-5°/0°$
④ ● Slotted tips; $\delta_{A,B,C}=20°/0°/-20°$; $\varepsilon_{A,B,C}=-10°/-5°/0°$

The model consisted of an inner rectangular wing which could be equipped at each wing-tip with up to 3 winglets. The slitting ratio was $\eta_o=0.714$ and the aspect ratio of the unslitted outer rectangular wing was $A=4.0$. The main wing and the winglets had symmetrical airfoil sections NACA 0015. The winglets were pointed from $2l/7$ at their basis to $l/7$ at their tip (l = chord of the inner wing) and could be arranged at certain stagger angles δ and at twisting angles ε which were constant along their span.

In Fig. 3 the drag coefficient c_D is plotted versus the lift coefficient c_l ($c_D=2D/\rho V^2S$; $c_l=2L/\rho V^2S$) for different configurations. The unslit rectangular wing (curve 1) has the lowest drag coefficients c_D. Slitting the wing-tips (curves 2, 3, 4) increases the drag coefficient at zero lift due to increased friction drag as mentioned earlier. Slitting the

wing-tips into a plane, untwisted system of winglets (curve 2) leads to an increase of drag and a reduction of maximum lift coefficient because of flow separations at the winglets. These effects have been clearly identified by means of flow vizualisation techniques. For the plane system of winglets these flow separations can be avoided by a proper twisting angle ε at each winglet. It turns out, that the best arrangement (curve 3) of winglets in the plane of the main wing has a slightly larger drag coefficient and about the same maximum lift coefficient as an unslit rectangular wing. This means that a tandem arrangement of winglets has no significant effect on the lift and drag characteristics. If, however, the winglets are staggered in height at the same optimum arrangement of twisting angles ε (curve 4), the drag is reduced by the same amount as indicated by the theoretical predictions according to chapter 3.

In a second graph in Fig. 3 the lift coefficient c_l is related to the quantity $c_D/c_l^{3/2}$, which is proportional to the velocity of sinking in the case of a gliding flight. It turns out from the experiments that the minimum value of the velocity of sinking is considerably reduced by staggering the winglets at the wing-tip in height.

The drag reduction according to the measurements (Fig. 3) lies in the same order of magnitude as predicted by the theory (Fig. 2). The values are not directly comparable because of the slight differences in geometry. Fig. 3 shows also that the moderate drag reduction can only be obtained by a proper adjustment of the winglets.

Discussion

The present theoretical and experimental investigations have shown that slotted wing-tips are devices:

(i) to increase static stability as a planform effect

(ii) to reduce induced drag by staggering the winglets in height.

The possible reduction of induced drag is moderate. It could also be achieved by a slight increase of wing span according to equ. (2). If the way of life of a bird allowed a slightly larger wing span to increase its aerodynamic efficiency, evolution might have developed the wings in this direction. Therefore, all seabirds as well as swallows, swifts and some other families have non-split pointed wings of large aspect ratio. If, on the other hand, the way of life of a bird restricts length of the wing span, slitting of the wing-tips and staggering of the winglets in height is a device to increase the aerodynamic efficiency. An example for this fact are the pheasants. Their span is so strongly limited that they have developed the largest number of winglets of all birds in order to achieve sufficient flight performance.

Apart from take-off and landing, all seabirds, swallows and swifts without slotted wing-tips as well as the pheasants, bustards and related families with highly slit wing-tips fly at a distinct point of their lift-drag-curve, see Fig. 3, for which their geometry has been developed by evolution. A large number of other bird families such as for instance storks, cranes, hawks and vultures use their wings in two different configurations: in gliding flight the wing span is reduced and the wing-tips are closed, whereas in soaring flight these birds fly with their maximum span and their wing-tips are slotted. This well-known behaviour can be interpreted as follows: in high-speed gliding flight the lift coefficient $c_l = 2L/\rho V^2 S$ is low and therefore the coefficient of induced drag is small. There is no need to reduce induced drag and therefore the wing-tips are closed.

Moreover, the wing span is reduced which increases the induced drag, but the main portion of drag is friction drag, which is kept low by a small surface 2S. In soaring flight the bird circles in thermals at low speed. In this flight condition the lift coefficient is high and the main portion of drag is induced drag. In order to keep induced drag small and thus to achieve a small sinking velocity the wing span has to be as large as possible and the wing-tips must be slotted.

Finally, the basic results reported here might also be important for certain periods of the flapping cycle of an even larger number of bird species. During the downstroke the wing produces negative induced drag, which is called thrust, see BILO (1971, 1972) and HUMMEL & MÖLLENSTÄDT (1977). If the bird's way of life has allowed a slight increase of the wing span, the wing is also closed within the flapping cycle during the downstroke, see e.g. snipes and waders. But in order to obtain a maximum of thrust from a wing of limited span, splitting of the wing-tips is a suitable device. It is well known that almost all songbirds are equipped with emarginated primaries and snapshots show that they are extremely spread during downstroke in flapping flight, see BILO (1971).

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On the Structure of the Wake of a Flying Bird

Nikolai V. Kokshaysky

Introduction

In order to move actively any organism or vehicle must apply some force to other bodies in the direction opposite to the direction of movement. In terrestrial animals as well as in terrestrial locomotion of birds, we can often observe the results of this force application in the form of the tracks in the substrate. It is possible to estimate the order of magnitude of mechanical forces involved in the movement from such tracks.

In a flying bird the situation is quite different. The medium in which it moves is deformed even by the slightest force and is incapable of retaining the residual deformations. From these properties of the air it follows immediately that no dynamometrical measurements of the forces exerted by a flying bird on the air are possible; the calculations derived from the wake flow field are thus the only reliable method of dynamical analysis. But the bird's wake is invisible. Although the wake is an important source of information on dynamics of active bird flight, it is not easy to deal with.

Quantitative data based on bird wake measurements and calculations are of interest in many respects. Indispensable for such investigations is the determination of what the wake looks like. Accordingly, the main purpose of the present study is to develop methods of wake visualization, and the recording and the demonstration of its general structure.

Methods of bird wake visualization and recording

Visualization of the wake of a flying Chaffinch *(Fringilla coelebs* ♂) and Brambling *(F. montifringilla* ♂) has been performed by means of multiple flash photography of small light particles forming a cloud through which the bird was forced to fly. Many kinds of visualizing agents were tried. Wood and paper dust produced with a grindstone was used most frequently. The mean sinking speed of paper dust in still air was 0.2 m/s. The birds performed their short flights initially in a plexiglass container (2 × 0.5 × 1 m) and then in a net cage (2.6 × 0.6 × 0.7 m). The generator for a series of flashes had been specially designed for this study by Mr. V. I. Petrowsky, who was very active also in conducting experiments, and was modified in the course of experimentation. It was triggered by one or two photorelays when the bird crossed an infrared beam. The frequency of flashes and their number per series were adjustable within a wide range. The most satisfactory results were obtained with frequencies of about 1 kHz and 7—8 flashes per series.

The experimental procedure was as follows. The room was darkened (only very faint illumination being retained) and the shutters of two photographic cameras providing side and front views of the bird's trajectory were opened. Then a cloud of visualizing particles was blown out through a long rubber tube from the container attached to the

A. N. Severtzov Institute of Evolutionary Animal Morphology and Ecology, Ac. Sci. USSR, Leninsky Prospekt 33, Moscow W—71 USSR.

top of the aquarium or the cage and the bird was flushed from the perch. When the flying bird had triggered the light generator, a series of flashes was emitted (Fig. 1).

The multiple images of individual visualizing particles on the photographs demonstrate their spreading in the direction of the movement, like the images obtained in more classical methods with constant illumination and prolonged exposures. The faster

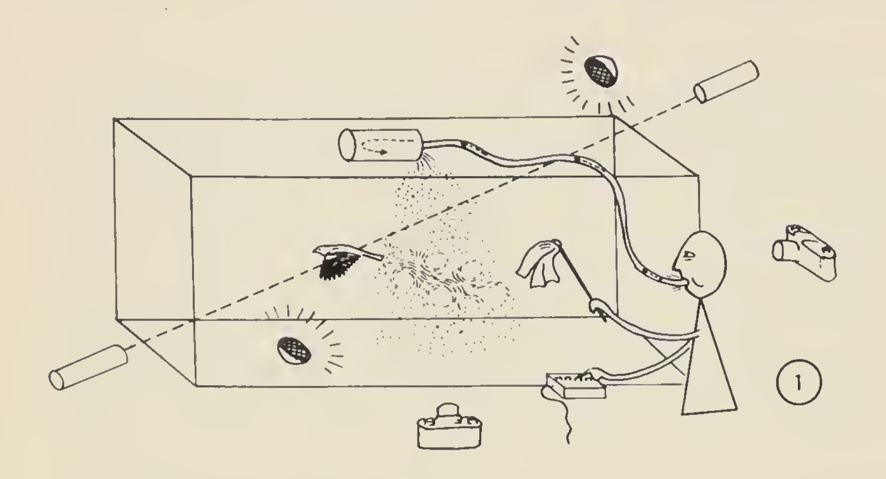


FIGURE 1. Experimental set up for visualization of the wake behind a flying bird.

a particle is moving the more elongated is the hatched line produced on the photograph. These lines represent an approximation to the trajectories of fluid particles. With the scale and flash frequencies known it is possible to calculate roughly a number of characteristic velocities in the wake flow field pictured in the photographs.

Results and discussion

The mode of flight performed by finches during the wake visualization experiments certainly approaches the so-called slow flight type. As revealed by filming of flights in the container, the Brambling (mass about 22 g) tended to hovering; in forward flight, horizontal speed was 1.8 m s^{-1} at a mean wing beat frequency of 17 Hz. The Chaffinch (mass about 21 g) developed 3 m s^{-1} at 18 Hz. The structure of the bird's wake is illustrated by the pictures of its side view received during flights performed in the cage (Fig. 2.1, 2.3). The form of particle cloud as well as illumination through a slotted aperture predetermine that the pictures represent longitudinal sections of the wake, i.e. its two-dimensional aspect. As particles are more dense than the air and are not deformable, their visualizing effect is in some respects weakened and in other accentuated. In particular, the central parts of vortices are free of particles as a result of a centrifugal force action. Only outside of the vortex core is this force balanced by a "lift force" (MERZKIRCH, 1974).

The two-dimensional aspect of a wake is interpreted as follows. At the beginning of downstroke, when circulation is building up around the wing, the wing sheds a vortex, which must be treated as a starting vortex; its rotation being opposite to circulation around the wing. At the end of the downstroke, when circulation is decreasing, the wing sheds an equal vortex rotating now in the direction of circulation. The event repeats at every full stroke, so that a vortex chain is formed. A jet flows backward between two rows of vortices. This interpretation agrees well with the theoretical computations of the structure of a flapping wing wake, which had been made for the first time, to my knowledge, by TH. VON KÁRMÁN & J. M. BURGERS (1935) and afterwards were strongly confirmed by V. V. GOLUGEV's studies (see KOKSHAYSKY, 1974, for further references).

An analysis of photographs depicting front (or rear) views of the wake, as well as general considerations of fluid mechanical properties of vortices, permits construction of the spatial structure of the wake behind a flying bird. It may be represented by a separate vortex ring for each wing stroke (Fig. 2.2). During the upstroke, the wings are folded in smaller birds producing practically no aerodynamic side forces. Formation of the vortex ring in the wake should occur only during the downstroke. This simplifies the configuration of the wake.

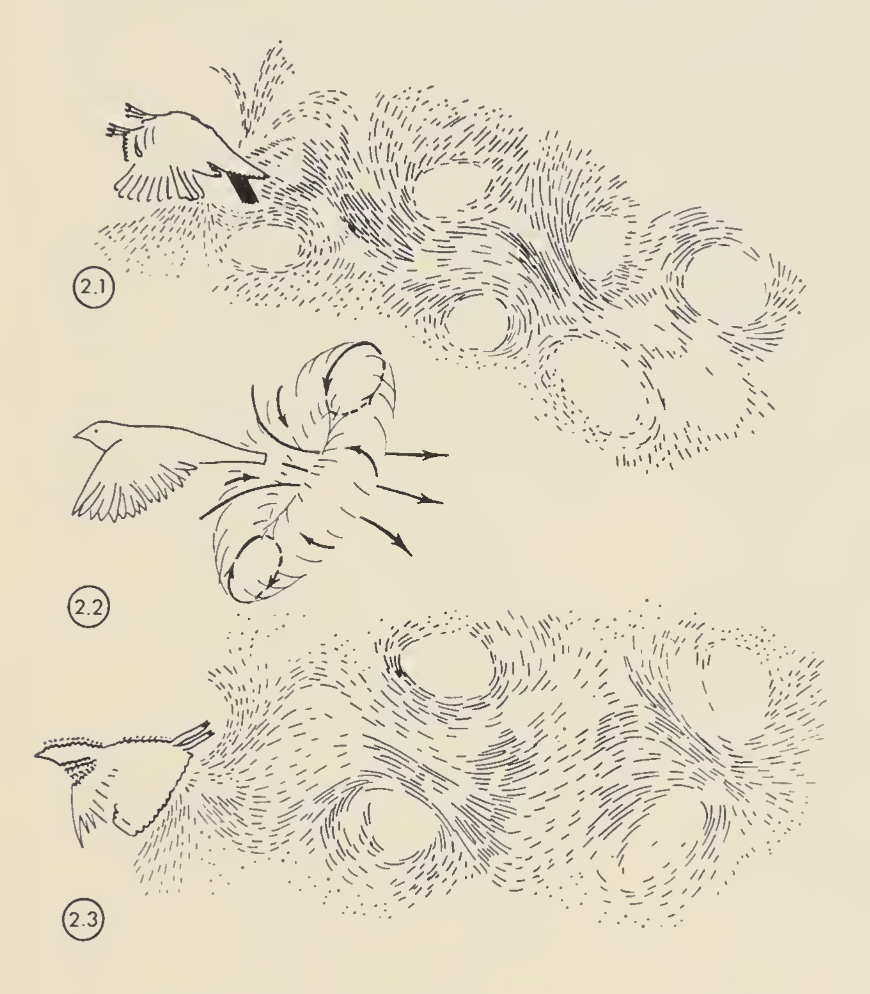


FIGURE 2.1 and 2.3. Outline drawings of wake flow visualization photographs. Pairs of plane vortices produced during successive wing-strokes of Brambling (1; three pairs) and Chaffinch (3; two pairs) are visible. The lengths of dashes do not always correspond exactly to the lengths of individual particle tracks.

FIGURE 2.2. Spatial structure of a flying bird's wake represented by a discrete vortex ring produced during the downstroke. Arrows indicate direction of flow rotation. Partly hatched circles with arrows are cross-sections of the vortex ring visible in two-dimensional side-views of the wake.

No attempts were made in this study to calculate the amount of aerodynamic work wasted in the wake. With the demonstration of the general structure of the wake, the task appears to be solvable, although some difficulties still exist. It is clear that precise measurements of velocity fields throughout the wake or the estimation of interaction between the rotating masses of fluid concentrated in the vortex rings and those moving in the form of jets will demand further and more accurate experimentation.

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Physiological and Energetic Adaptations of Flying Birds, Measured by the Wind Tunnel Technique. A Survey

H.-J. ROTHE and W. NACHTIGALL

Which physiological parameters permit birds to produce sufficient energy for flight? The main method in use to measure energetic parameters is the wind tunnel technique. Physiological and metabolic investigations take place with birds flying free in a test section of a wind tunnel (BAUDINETTE et al., 1976, and many others). Ambient conditions can be modified and different analysers regardless of their size can be connected to the flying birds by wires or tubes (Fig. 1).

Analysing the contents of the exhaled air and the metabolic and catabolic concentration in the blood is very important for the investigation of metabolic and energetic problems. The method most often used is the following: Birds are trained (NACHTIGALL & ROTHE, 1978; TUCKER, 1969) to fly in the test section of a wind tunnel. They wear a mask by which the exhaled air is sucked off and brought to the gas analysers (Fig. 1). In this way, oxygen, carbon dioxide and water content of the exhaled air can be meas-

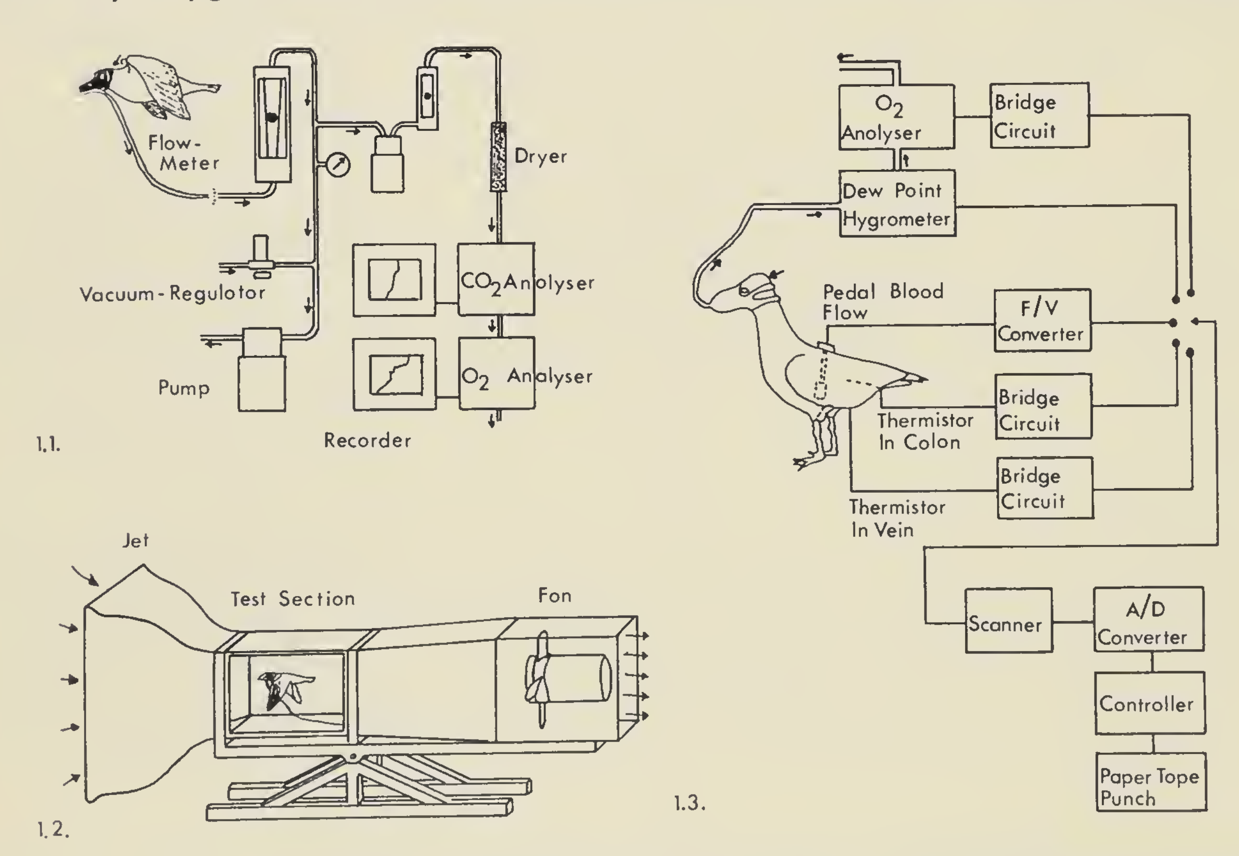


FIGURE 1.1. TUCKER's analyzing equipment for the measurement of carbon dioxide and oxygen exchange rates (TUCKER, 1969). 1.2: Tucker's wind tunnel designed for his experiments with flying birds (TUCKER, 1969). 1.3: BAUDINETTE's diagram of instrumentation used to record blood flow in the ischiatic artery, core and venous temperatures, respiratory water loss and oxygen consumption (BAUDINETTE et al., 1976).

ured. Additional probes and catheters can be fixed on the bird to register temperature, ECG, EMG, heart frequency, blood pressure, blood contents etc. (BAUDINETTE et al., 1976, and many others). If the bird's fuel is known and oxygen consumption and car-

Zoologisches Institut der Universität des Saarlandes, 6600 Saarbrücken, Bundesrepublik Deutschland

bon dioxide production are measured, the energy production of the organism can be estimated. If, for example, fat is the energy source, a bird can produce $4 \cdot 10^4$ Joule (9.56 kcal) from 1 g fat burned with 2000 ml oxygen. A pigeon of about 400 g body weight could fly 11.8 kilometers with 1 g fat, if the fat is burned completely and if effectivity of the flight muscles is about 20 % (JAMES & MEEK, 1976). The amount of carbon dioxide expired and of oxygen consumed (respiratory quotient = RQ) indicates the type of fuel burned, e.g. when RQ = 0.7 only fat was used, when RQ = 1.0 only carbohydrates were burned and when RQ is more than 1, energy is produced anaerobically.

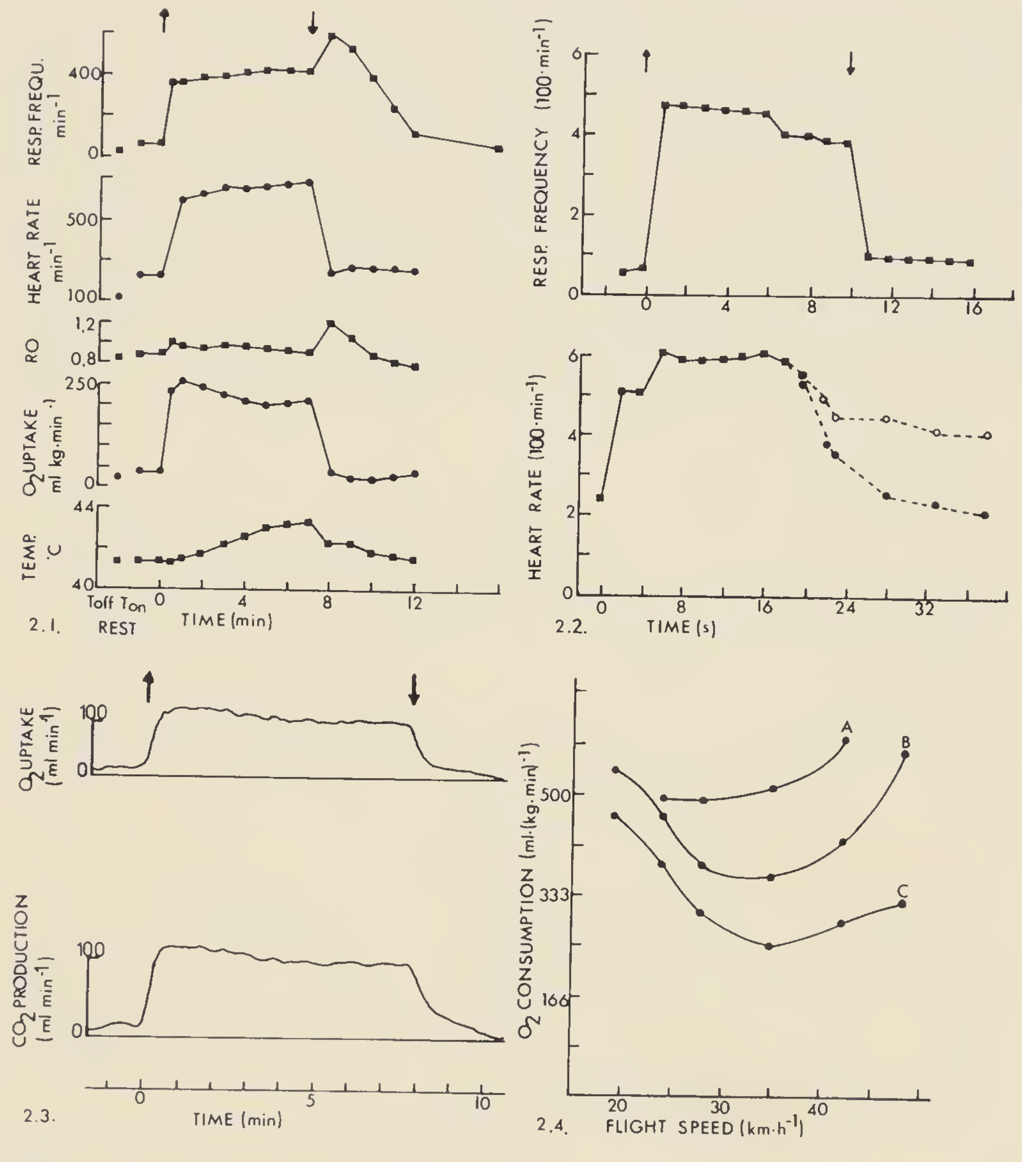


FIGURE 2.1. Different physiological parameters measured on pigeons flying in a wind tunnel. Arrows indicate points of take-off and landing. Resting values were taken when the tunnel was turned off (T.off) and when the tunnel was on (T.on) (BUTLER et al., 1977). 2.2: Respiratory frequency and heart rate in spontaneously flying pigeons. After landing white king and homing pigeons showed significant differences in the heart rate (solid circles heart rate of homing, open circles heart rate of white king pigeons) (BUTLER et al., 1977). 2.3: Simultaneous recording of oxygen uptake and carbon dioxide production of a pigeon (mass 0.48 kg) before, during and after a 8 min flight at 10 m/s (36 km/h) (BUTLER et al., 1977). 2.4: Mean oxygen consumption of two budgerigars during level (A), 5° ascending (B) and 5° descending (C) flight at different speeds (TUCKER, 1969).

Flight metabolism is rather high. Thus the respiration frequency of a flying budgerigar increases in relation to the flight speed up to 200 breaths/minute (TUCKER, 1967),

the pigeon up to 411 breaths/minute (Butler et al., 1977) (resting condition: 19.7). Respiration quotients from 0.7 up to 1.0 were measured with some more than 1.0 in the case of the pigeon. While there was no relation between the respiration and the wing-beat frequency in budgerigars a 1:1 relation was found in pigeons. This relation does not seem to be unusual because relations from 1:1 up to 5:1 were found in other bird species. Some species were found to fly with different constant relations in the ranges from 1:1 up to 5:1 (Berger et al., 1974). During flight, oxygen consumption is dependent on speed and flight angle and amounted to 12 (budgerigar flying horizontal at 35 km/h [Tucker, 1969]), 58 (laughing gull [Tucker, 1972]) and 88 milliliters (pigeon flying horizontal at 36 km/h [Butler et al., 1977]). The oxygen consumption of the budgerigar shows a marked dependence on the speed and angle of flight, whereas this dependence is not so evident in laughing gulls and fish crows (Fig. 2.4, 3.1.1.).

The flight angle greatly influences the oxygen consumption of birds flying in a wind tunnel. Gulls and fish crows were not able to fly in wind tunnels at positive angles (simulation of ascending flight) while wearing a mask. Generally a bird needs more oxygen for ascending than for descending flight. This is also relative for the production of carbon dioxide during flight. CO_2 production increases up to 9.4 ml/minute in budgerigars (Tucker, 1969) and up to 80.9 ml/minute in pigeons (Butler et al., 1977) (Fig. 3).

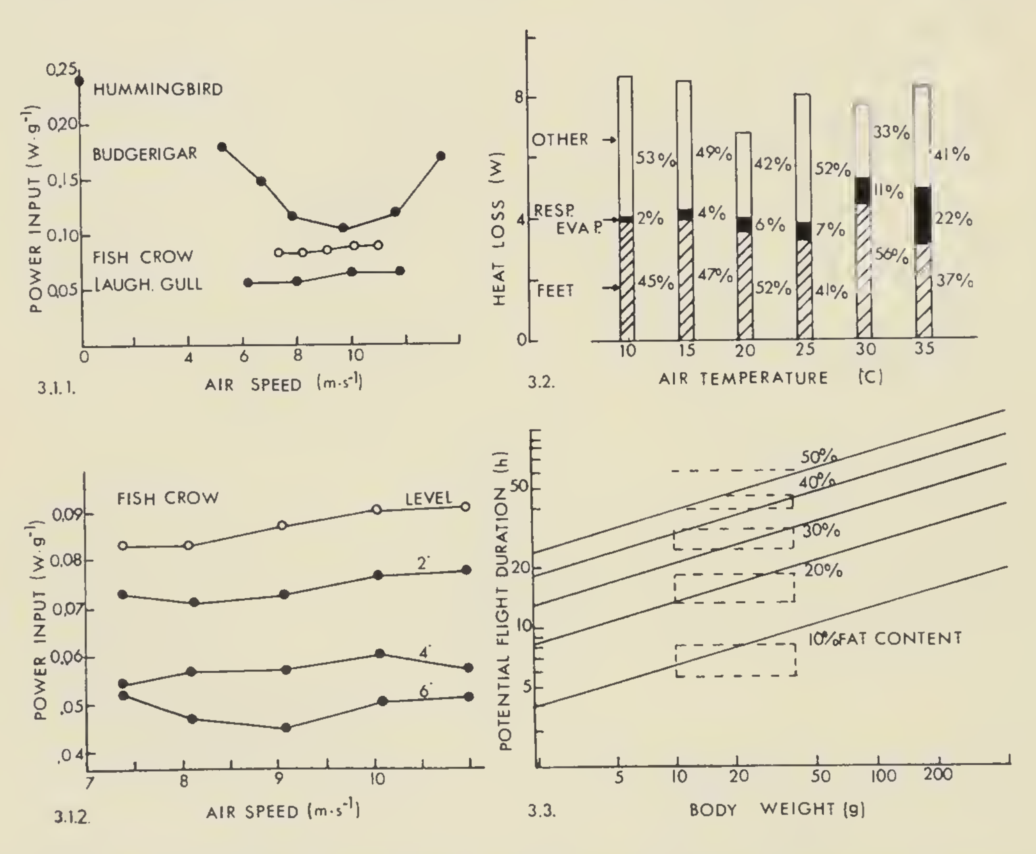


Figure 3.1.1. The relationship of power input to air speed in three species of birds during horizontal flight and in a hovering hummingbird (Bernstein et al., 1973). 3.1.2. The relationship of power input to air speed in the fish crow during flight at different descent angles. Values for horizontal flight are calculated (Bernstein et al., 1973). 3.2: Partition of heat loss for herring gulls at rest at various temperatures (Baudinette et al., 1976). 3.3: Calculated potential flight duration in relation to fat content and body weight. Rectangles and dashed line include ranges given by Odum (1961) and Berger et al. (1973).

When transformed into mechanical energy by the muscles, a great deal of the chemical energy used while flying is lost as heat. If this heat could not be removed it would

lead to an increase of body temperature. The core temperature of birds is generally much higher than that of mammals, being about 41 °C. Birds are not so sensitive to overheating, pigeons for example can tolerate core temperatures of more than 51 °C for a short time (Calder et al., 1977). Nevertheless overheating of the bird during sustained flight must be prevented. Heat loss by transpiration is not possible because of the lack of sweat glands. Thermoregulation takes place by radiation, convection and water evaporation in the respiratory system and through the skin (Berger et al., 1974). By means of temperature measurements of the different parts of the body and analysis of the water content of the exhaled air, the heat produced by the muscles and the effectivity of the latter can be determined if the physical performance of a bird during flight is known. Assuming that $2.4 \cdot 10^3$ Joule = 0.58 kcal are necessary for the evaporation of 1 g water, one can calculate the heat dissipated by water evaporation. An inactive pigeon loses 0.38 g water through the exhaled air, a budgerigar flying horizontally at 35 km/h at an ambient temperature of 10—20 °C loses 0.7 g water/h and a herring gull loses 1.08 g water/h when flying horizontally at a temperature of 20 °C. This corresponds to an energy lost as heat of $0.7 \cdot 10^3$ Joule/h = 0.17 kcal/h = 0.1 W in pigeons, $1.7 \cdot 10^3$ Joule/h = 0.41 kcal/h = 0.5 W in budgerigars and $2.5 \cdot 10^3$ Joule = 0.6 kcal/h = 0.7 W in herring gulls (Baudinette et al., 1976; Butler et al., 1977; Tucker, 1969). The high body temperature facilitates radiation and convection through the body surface if the ambient temperature is relatively low.

At low or medium ambient temperatures, 80 % of the heat produced can be delivered by the skin. In flying pigeons this is between 1 and 2 Joule/cm^2 body surface during a 1 hour flight (Berger et al., 1974). This corresponds to a 6—8 fold increase of the resting level and is therefore within the range of the increasing heat production during flight.

The enormous increase of metabolism is obviously connected to the increase in cardiovascular activity. The heart beat frequency can reach as much as 4 times the resting level (Berger et al., 1974). This increase in cardio-vascular activity is important not only for supplying all tissues with oxygen, but also for the removal of carbon dioxide and heat from the different muscles. An increase in flight muscle activity leads to a larger fuel requirement. Fat is the source of energy for sustained muscle activity and is either stored directly in the muscles and adipose tissue or is directly synthesized from the food by the liver and then transported by the blood as triglycerides or free fatty acids. Strong muscle activity increases the glucagon level, which raises the concentration of triglycerides, free fatty acids and sugar in the blood. Contrary to mammals, the liver in birds can synthesize fat and fatty acids. 77 % of the energy required by a pigeon during sustained flight is produced by the oxidation of fat (George et al., 1966) (RQ must be lower than 1). A small amount of this fat is, as mentioned above, stored in the muscles. About 20 % of the dry weight of the pectoralis muscle in pigeons is fat (James & Meek, 1976). Besides fat, glycogen as an energy source is also stored there. According to the different muscle demands, glycogen or fat are converted into energy by the different muscle fibers. Principally two kinds of muscle fibers can be found in the pectoralis muscle of pigeons, red and white muscle fibers (George et al., 1966). They differ in the speed of contraction and in their morphological and histochemical appearance. White muscle fibers are mainly fast ones, and are primarily used for thermal shivering. They contain glycogen as energy source, have very little mitochondria

and nearly no myoglobin. Furthermore they have no lipases and other enzymes of the fat and fatty acid metabolism. White fibers can work anaerobically and are not used for sustained work. Red muscle fibers contain lipids, have a high myoglobin content and a large amount of mitochondria. These fibers are narrower than the white fibers and outnumber the white in the pectoralis muscle of pigeons. They have lipases and the other enzymes of fat metabolism but not those of glycolysis. Their fuel is fat, they work aerobically, have many surrounding blood vessels and are used for sustained muscle activity. Besides red and white fibers, some bird species have intermediate fibers with characteristics of the two former types.

Normally only fat and carbohydrates are used as muscle fuel in birds. Proteins will be oxidised for energy only in exceptional cases such as starvation. Fat is the usual fuel for sustained flight activity. It is therefore not surprising that before migrating, birds store great amounts of fat which will be entirely consumed during migration (ODUM et al., 1956 & 1961). In brief and fast muscle activities, carbohydrates are often used as energy source. These activities are often anaerobical as one can see at RQ's greater than 1 and at high lactate concentrations in the blood. This was only measured in pigeons flying in a wind tunnel. During horizontal flight at 36 km/h the lactate concentration increased from 9 to 59.8 mg % and the respiratory quotient was sometimes more than one. Contrary to bird species whose pectoralis muscle consists only of red fibers, the pigeon pectoralis muscle with 85.9 % red and 14.1 % white fibers (GEORGE et al., 1966) is capable of short term anaerobic activity.

Although experiments with birds flying in a wind tunnel can only produce an approximation of the flight conditions of a free flying bird, this is the best method of obtaining data. But several points must be taken into consideration when interpreting the results of the experiments. The bird has to fly in a relatively small space, must tolerate the noises of the fan motor and is in an optically motionless and monotonous environment. The bird moves against the wind; in turbulent tunnels this may cause flight configurations which differ from those in nature. We have observed that pigeons learned to fly in our tunnel more easily and in less time, when 3 additional laminar

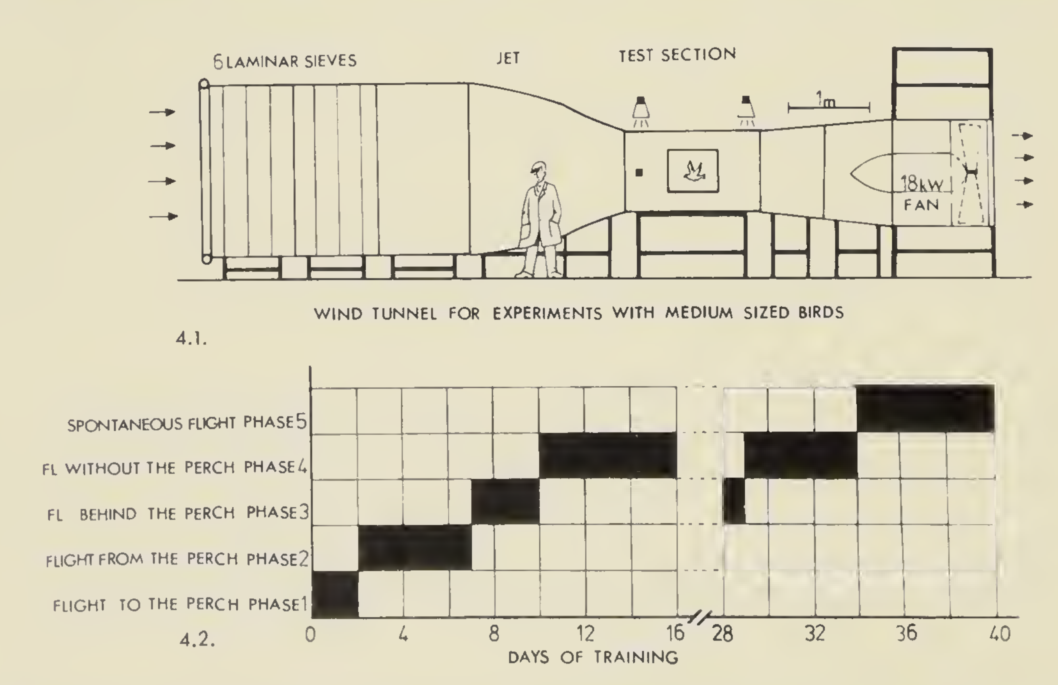


FIGURE 4.1. Wind tunnel used at Saarbrücken University to analyse pigeon's flight. Drawn to scale. 4.2. Training diagram of pigeon no. 4.

sieves (Fig. 4.1) were installed and turbulence was greatly diminished. Birds warmed up much slower and started panting only after longer periods of flight or did not at all. Up to date, about 20 birds of different species have been tested in various wind tunnels, but the different physiological parameters have not yet been correlated with the individual flight behaviour of the birds. We observed in our experiments with 11 pigeons (4 of which flew between 10 and 60 minutes at a speed of 50 km/h), that the behaviour of the individual pigeons varied extremely. None of the pigeons flew stationary in the center of the test section. Each pigeon developed its own style of flight by which it could be identified. This style was not always the most economical one under the given conditions, so that measurements of temperature and weight loss showed marked variation. This must be taken into consideration when linear extrapolations are made and averages calculated.

Another important factor in wind tunnel experiments is the physical condition of the bird. If pigeons are kept in an aviary where they cannot fly, one hour's training in the wind tunnel will not be sufficient to keep the bird as fit as it would be when free. By intensifying their daily training our pigeons were able to fly for long periods (> 1 h) in the wind tunnel, but a three day interruption in training reduced their ability to fly in the tunnel considerably (Fig. 4.2). Besides this differences in body weight and wing span cause differences in their achievements. Birds of less than 400 g body weight and with spans about 0.5 m were the best flyers. In spite of such difficulties arising with the wind tunnel method, no alternative can be suggested now or in the near future for the investigation of the physical and physiological parameters of bird flight.

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SYMPOSIUM ON
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Relationship between Circadian Activity Patterns and Gonadal Function: Evidence for Internal Coincidence?

Eberhard Gwinner

Introduction

From investigations in several bird species it has become clear that a circadian rhythmicity plays a central role in the measurement of photoperiod. The most striking evidence for such a mechanism comes from "resonance" and "interrupted night" experiments indicating that the photoperiodic reaction depends neither on the duration of light time nor the duration of dark time but on the temporal relationship between light and an endogenous circadian rhythmicity (see Farner & Lewis 1971, Follett 1973, Gwinner 1975a for reviews). These findings are consistent with a model, first proposed by Erwin Bünning in 1936. This model assumes that organisms are equipped with a circadian rhythm of photosensitivity, and that photoperiodic reactions are induced (or inhibited) when a particular phase of that rhythm is exposed to light. Apart from birds, evidence in support of Bünnings hypothesis is available for several other groups of plants and animals (for reviews see Danilevskij et al. 1970, Saunders 1976, Bünning 1977).

The intricacies and implications of Bünning's model have been discussed by Pittendrigh (Pittendrigh & Minis 1964, 1971; Pittendrigh 1966, 1972). He pointed out that in Bünning's initial model light plays a dual role in that it (1) entrains a circadian rhythm of photosensitivity and (2) induces a photoperiodic response when it falls on a particular phase of that rhythm. Since in this version of the model the photoperiodic reaction eventually depends on the coincidence of the external light signal with a circadian phase, Pittendrigh (1972) termed this class of models "external coincidence" models. In principle, however, most phenomena could be interpreted just as easily by assuming that light only entrains the circadian rhythmicity without exerting an additional inductive effect. In this case photoperiodic reactions might depend on particular states of the circadian system which, in turn, result from different entrainment patterns. Specifically, it has been proposed that photoperiodic alterations change the phase-relationship between two or more circadian oscillators within the organism and that a photoperiodic reaction occurs when a particular phase relation is established (e.g., Tyshchenko 1966, Pittendrigh 1972, Gwinner 1973, Pittendrigh & Daan 1976, Dolnik 1976). Since in this new version of the model the photoperiodic reaction depends on the coincidence of particular phases of two or more internal rhythms, Pittendrigh (1972) has called these models "internal coincidence" models.

An important prediction of the latter version of the model (regardless of whether internal coincidence or any other changes in the circadian system are assumed, Gwinner 1973) is that it should be possible to induce photoperiodic reactions even in the absence of light, when the circadian system is appropriately changed, e.g., by Zeitgebers other than a lightdark cycle. Experiments of that kind have been performed recently by Saunders (1973). He succeeded in inducing photoperiodic reactions by

Max-Planck-Institut für Verhaltensphysiologie, D—8131 Andechs, Bundesrepublik Deutschland

exposing insects to temperature instead of light cycles. Another approach has been used by WOLFSON (1966) whose results and hypothesis will be discussed in the following paragraphs.

WOLFSON's Hypothesis

In his basic experiment, WOLFSON exposed 11 photosensitive Slate-colored Juncos *(Junco hyemalis)* to a stimulatory 16-hour photoperiod for 8 days. 4 birds were then transferred to continuous darkness (DD) and 7 to a 9-hour photoperiod. After 18 days in these conditions the DD birds had enlarged testes (mean weight: 117.9 mg) whereas the short-day birds had regressed testes (7.9 mg). Moreover, the DD birds showed a clear tendency to maintain the pattern of activity present during the initial long-day exposure throughout the experiment: their daily activity time α was longer than that of a group of White-throated Sparrow *(Zonotrichia albicollis)* which was used for comparison and placed in DD after pretreatment with a short photoperiod (and which showed no testicular response). Moreover, among the long-day pretreated Juncos, those with largest testes also showed the longest α_s. From these and some additional experiments WOLFSON concluded that "the light-dark cycle appears to serve as information which the bird uses to measure the length of the day". This measurement is then translated by the hypothalamohypophyseal system such that when the days are "long" a daily gonadotropic response occurs. When they are "short", it does not. Decisions that long days are present can apparently be made in continuous darkness, and it is likely that the duration of activity during continuous darkness is a manifestation of and/or contributes information for this measurement.

Despite some shortcomings in the design of these experiments (e.g. the small number of birds; the lack of information about testicular conditions before and after long-day treatment) WOLFSON's results still suggest an internal coincidence mechanism. PITTENDRIGH & DAAN (1976) interpreted the results from the birds placed in DD after long-day pretreatment as "the effect of a long photoperiod establishing a set of phase relations between constituent oscillators that induce gonadal growth, and the inertia of the system, reflected in after-effects, retaining that inductive state in constant darkness. Short days on the other hand, have an immediate positive action in destroying the inductive phase-relation between morning and evening oscillators."

I have carried out experiments to investigate the extent to which WOLFSON's results are more generally valid and whether they, indeed, support an internal coincidence model. This was done by examining 4 major questions related to WOLFSON's proposition, asking: (1) Is DD a less potent stimulus for the induction of testicular regression than short photoperiods? (2) Is there evidence that long-day information is stored and maintained in DD or LL? (3) Is there a correlation between circadian activity time under constant conditions and the gonadal state? and (4) If so, to what is this correlation due?

Differential effects of short photoperiods and DD on testicular regression

To test whether DD is a more favourable condition for testicular maintenance than a short photoperiod we carried out two experiments with male White-crowned Sparrows *(Zonotrichia leucophrys gambelii)*. In both experiments, photosensitive birds were

initially exposed to a long 20-hour photoperiod for different periods of time and subsequently transferred to either constant dim light of a non-stimulatory intensity or a short 6-hour photoperiod. The results are presented in Figure 1. They show that after transfer to DD, testicular size of the long-day pretreated birds was maintained at a high level for some time; compared with the birds transferred simultaneously to short days regression was significantly delayed.

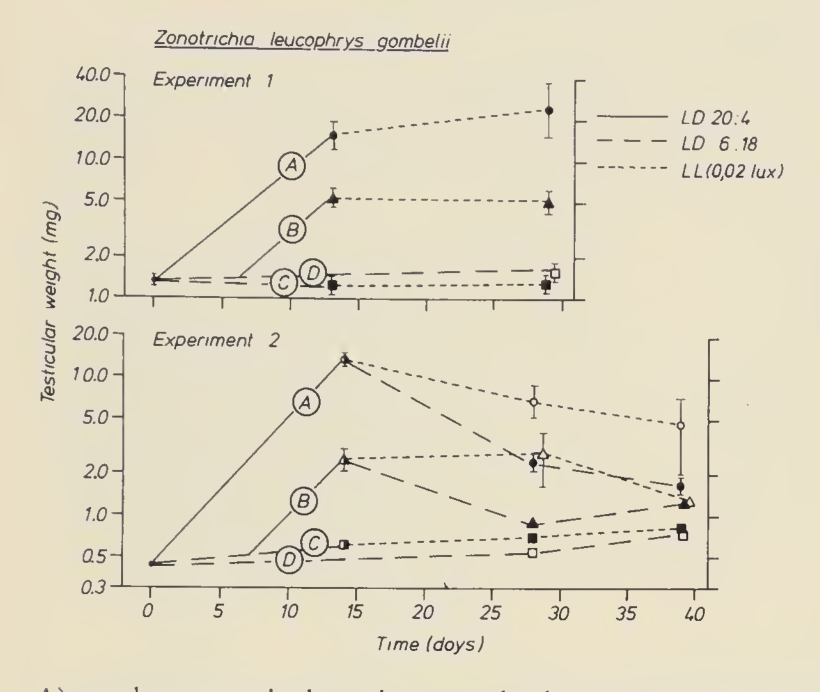


FIGURE 1. Results of two experiments with White-crowned Sparrows carried out to investigate the effects of continuous dim light and a short photoperiod on testicular regression. All birds were exposed to a short 6-hour photoperiod prior to the beginning of the experiments. They were highly photosensitive when transferred to experimental conditions (March 3 in experiment 1; January 7 in experiment 2). Birds of groups A and B were exposed to a stimulatory 20-hour photoperiod for about 1 (group B) and 2 (group A) weeks respectively; subsequently they were transferred either to continuous dim light (all birds in experiment 1 and about half of the birds in experiment 2: LL 0.02 lux; dotted line) or to a short 6-hour photoperiod (about half of the birds in experiment 2: LD 6;18; dashed line). Birds in group C were maintained in the short photoperiod for about 2 weeks and then transferred to continuous dim light. Birds of groups D served as short day controls. Samples of 6 to 10 birds were sacrificed at the times indicated and their testes were weighed. Mean testes weights with standard errors of the means are given. — The dim light is not stimulatory as shown by the testicular development of groups C but it is effective in maintaining testes size at a high level for at least two weeks in experiment 1, and induces slower regression than the short photoperiod in experiment 2. On day 28, mean testicular weights of both groups of birds transferred from the long photoperiod to dim light, are significantly larger than in the respective control groups transferred simultaneously to the short photoperiod ($p < 0.01$, MANN-WHITNEY U-test).

Results similar to those depicted on Fig. 1 have been obtained by TUREK (1978) in another study on White-crowned Sparrows and by FARNER et al. (1977) in experiments with the House Sparrow *(Passer domesticus)*. Evidence suggesting that the testes of House Sparrows may even continue to grow after transfer to DD has already been obtained by VAUGIEN & VAUGIEN (1961).

Effects of previous photoperiod on activity time in DD or LL

Fig. 2 shows activity recordings of 2 White-crowned Sparrows from experiment 1 which were pretreated with a 6-hour or 20-hour photoperiod before being placed in continuous dim light. It is clear that the long day pretreated bird retained a longer α than the short day pretreated bird. This was generally true for the birds of both experiments with White-crowned Sparrows as shown in Fig. 3. Similar results were also obtained in an experiment with Golden-crowned Sparrows (Fig. 3, experiment 3).

Here, both, intact and castrated males, first maintained in a long photoperiod, had a longer α in DD than intact conspecifics pretreated with a short photoperiod.

A temporary retention of α exhibited under previous conditions of entrainment when placed in DD has also been reported in mammals (PITTENDRIGH & DAAN 1976). A large body of data on various vertebrate species investigated in our laboratory suggests that this is a common phenomenon.

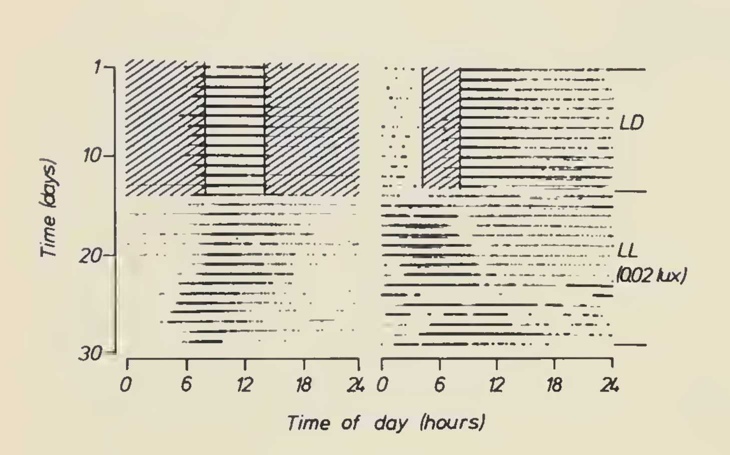


FIGURE 2. Activity recordings of two White-crowned Sparrows of experiment 1 (see Fig. 1). Each horizontal line represents the activity record of one day. Records of successive days are mounted underneath each other. Vertical marks indicate activity within one minute time intervals. During times of intense activity the marks fuse into a black block. During the first two weeks the bird on the left was maintained in a 6-hour photoperiod, that on the right in a 20-hour photoperiod. Then both birds were transferred to continuous dim light (0.02 lux).

It should be mentioned here, that not only α depends on previous photoperiodic conditions but other parameters of circadian rhythms as well, especially the circadian period τ. This is apparent in Figs. 2 and 3 which show that long day pretreated birds had longer τ's than short-day pretreated birds. Such "after effects" of photoperiod and other Zeitgeber properties on τ are well known; for a recent discussion see PITTENDRIGH & DAAN (1976).

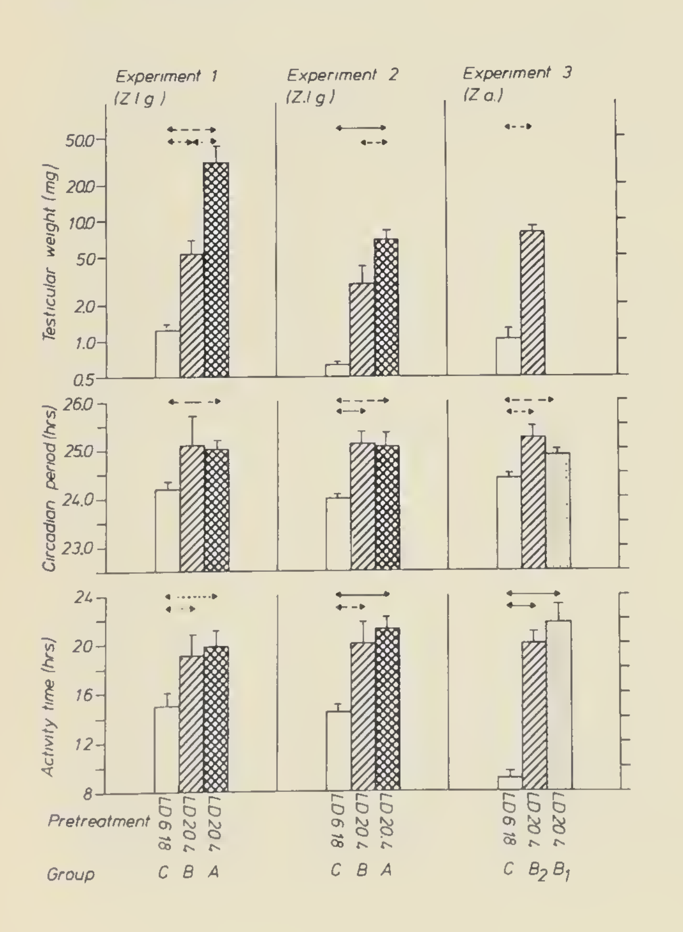


FIGURE 3. Experiment 1 and 2: Testicular weight, circadian period τ and circadian activity time α of White-crowned Sparrows kept for about 2 weeks in continuous dim light following exposure to either a 20-hour or a 6-hour photoperiod. These experiments are identical with experiments 1 and 2 in Figure 1. Data are from those birds of groups A, B and C which were exposed from day 13 to 29 (experiment 1) and from day 14—28 (experiment 2) to dim light and were subsequently sacrificed. In experiment 3, photosensitive golden-crowned sparrows were kept for 14 days in constant darkness following 25 days of exposure to a 6-hour photoperiod (group C) or a 20-hour photoperiod (groups B_1 and B_2). Birds of group B_1 had been castrated prior to the beginning of the experiment. — Arrows indicate significant differences between group means (◀—▶ $p < 0.001$; ◀——▶ $p < 0.01$; ◀— . . . —▶ $p < 0.05$).

Correlations between circadian activity parameters and gonadal state

In the experiments with crowned sparrows discussed before, both testis size and α had higher values in the long-day pretreated birds than in the short-day pretreated birds. Hence, testis size and α are also positively correlated with each other.

A positive correlation between these two parameters has also been found in the European Starling *(Sturnus vulgaris)* in another type of experiment. Here groups of male birds were transferred to continuous dim light or to continuous darkness at various times of the year. Depending on whether testes developed or not α either increased or remained more or less constant (GWINNER & TUREK 1971, GWINNER 1974, 1975 b). Fig. 4 shows examples of the activity recordings of birds with growing testes.

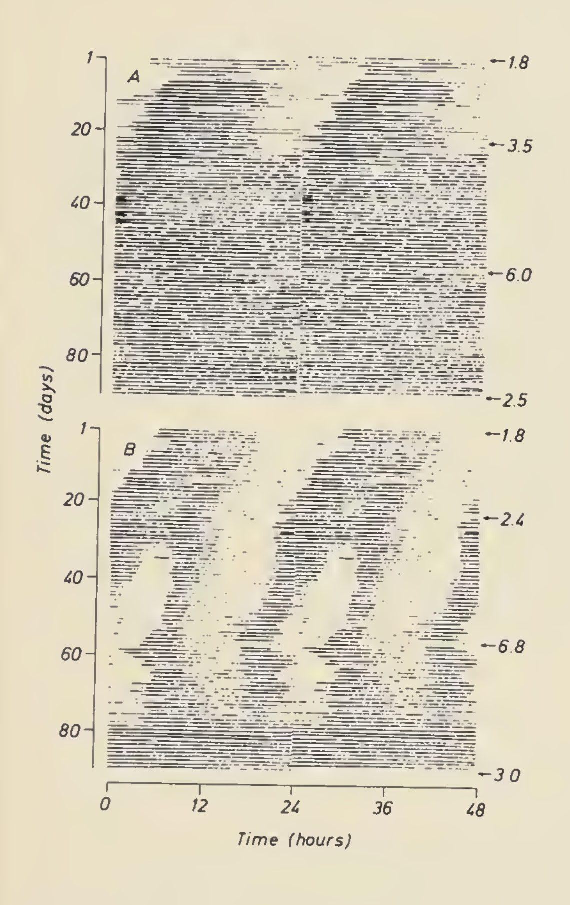


FIGURE 4. Activity recordings of two male European Starlings kept in continuous light of about 0.7 lux. To facilitate inspection of the data the records have been double plotted on a 48-hour time scale. Numbers at the right hand margin give the testicular widths (in millimeters) measured by laparotomy at the days indicated by the arrows. For further explanations see Fig. 2 (after GWINNER 1974).

Even in Starlings in which a second testicular cycle recurred after about one year in LL, α increased when the testes began to grow (GWINNER 1973). A similar relationship between testis size and α was also found by RUTLEDGE (1974) in the European Starling. Moreover, some of the results obtained by HAMNER & ENRIGHT (1967) in the House Finch *(Carpodacus mexicanus)* suggest longer α's in birds with large testes.

Causes of the relationship between circadian activity parameters and gonadal state

The results presented support WOLFSON's hypothesis to the extent that they show a positive correlation between α and gonadal state. The final question arises; to what is this correlation due? Here, at least 3 possibilities must be considered: (1) changes in the circadian system might affect the reproductive condition (WOLFSON's suggestion); (2) changes in the reproductive state might affect the circadian system; or (3) both, the reproductive state and circadian system might be affected independently by a third variable.

Up to now, good experimental evidence has only been produced for alternative (2). The most convincing experiments were with male European Starlings, indicating that castration prevents the increase in α normally occurring when intact photosensitive birds are exposed to LL. If, however, castrated birds are injected with testosterone, α lengthens immediately and in a manner similar to normal birds with growing testes (Fig. 5, GWINNER 1974, 1975). Preliminary results suggest that the same holds also true for birds entrained to a 24-hour light-dark cycle. Diagrams a and b in Fig. 6 show the spontaneous lengthening of α (resulting in the development of nocturnal activity) in male Starlings whose testes began to grow after transfer to a 12-hour photoperiod.

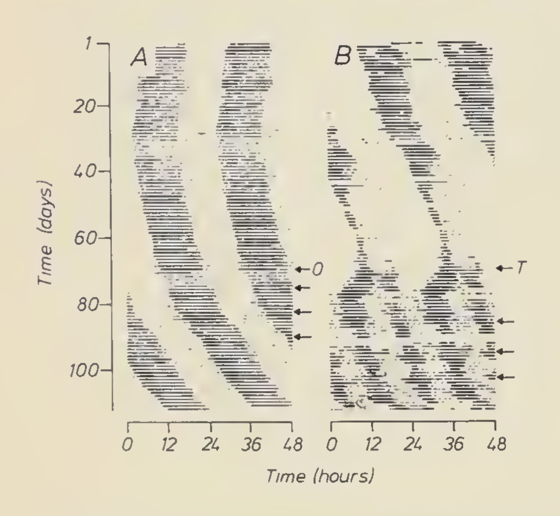


FIGURE 5. Activity recordings of 2 male European Starlings kept in continuous light of about 0.2 lux. Both birds were castrated prior to the beginning of the experiment. Starting on day 70 the birds were injected on the days indicated by arrows either with 0.1 ml of sesame oil (0, bird A) or with 2.5 mg testosterone dissolved in 0.1 ml of sesame oil (T, bird B). For further explanations see Fig. 2 (after GWINNER 1974).

Such an increase in α is not evident during the first 30 days of the activity record in the castrated Starling shown on Fig. 6 c and d. However, after testosterone injections, the activity patterns changed and became similar to those of the intact birds with growing testes. — Effects of sex steroids on circadian activity rhythms have also been shown in mammals (e.g., DAAN et al. 1975).

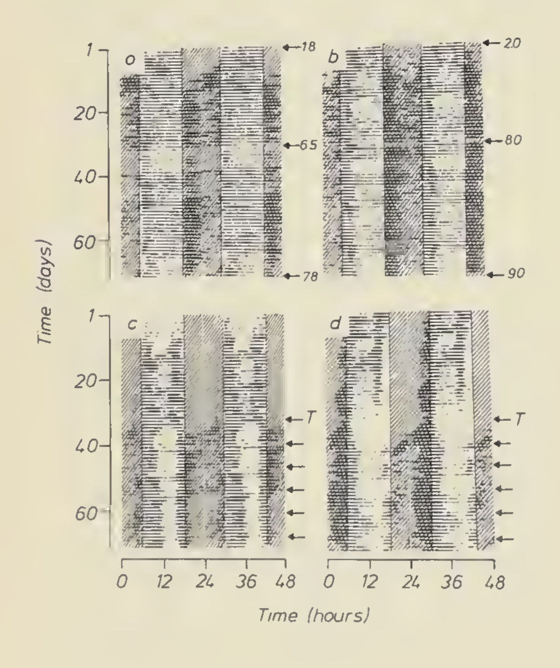


FIGURE 6. Activity recordings of 4 male European Starlings kept under a constant 12-hour photoperiod (LD 12:12, 200:0.05 lux). The 12-hour dark period is indicated by shading. a, b: records of intact birds in which testes began to grow following transfer to experimental conditions. Numbers at the right hand margin indicate the testicular width (in millimeters) measured by laparotomy at the days indicated by the arrows. c, d: records of birds that had been castrated prior to the beginning of the experiment. Starting day 32 they were injected on the days indicated by arrows with 2.5 mg testosterone dissolved in 0.1 ml of sesame oil (T). For further explanations see Fig. 2.

Conclusions

The results presented in the previous paragraphs confirm WOLFSON's initial observations in so far as they show: (1) that DD is less effective in inducing testicular regression than at short photoperiod (although significant growth has apparently never been rigourously documented under such conditions): (2) that the activity time of birds

transferred from a long photoperiod to continuous light or darkness is longer than in birds released from a short photoperiod to such conditions; and (3) that α and testis size are positively correlated with each other. On the other hand, no clear evidence is available supporting the hypothesis proposed by Wolfson on the basis of such findings: that the correlation between α and testis size is due to effects of the system controlling α on the mechanisms responsible for testicular maintenance. Indeed, this proposition has been considerably weakened by the inverse finding that testicular hormones induce a lengthening of α. At present time it appears as though all the available data demonstrating longer α's in birds with large gonads than in birds with small gonads (including Wolfson's own results) can be interpreted as the results of effects of sex steroids on the circadian system. Hence they provide no evidence in support of Wolfson's hypothesis or any other internal coincidence model.

There remain, however, two sets of findings that deserve further attention because they suggest that the situation may be more complex and that Wolfson's hypothesis certainly should not be rejected on the basis of the results discussed above. The first one is the result shown in Figure 2 that even castrated Golden-crowned Sparrows pretreated with long photoperiods have longer α's during their freeruns in dim light than birds pretreated with short photoperiods. This indicates that at least under these particular conditions a long α is not due to the action of gonadal hormones alone. Instead, it probably constitutes a more direct reflection of the previous entrainment pattern which was retained for some time in DD. It seems likely, therefore, that at least one of the components of the mechanism suggested by Wolfson — the storage of information about α — may, indeed, exist.

The second finding of potential impact is the observation made in at least 4 independent studies, that testes regress more slowly in birds transferred from long days to DD than in birds transferred from the same conditions to a short photoperiod. These results can, indeed, be accomodated easily with the hypothesis that long-day information is not only retained but also used in birds transferred to DD or LL, whereas it becomes extinguished in birds transferred to short days as they establish a new entrainment pattern. It should be emphasized, however, that alternative interpretations in terms of external coincidence models are also possible. For instance, it is conceivable, that DD or dim light is a "neutral" condition and that short days actively promote testicular regression; i.e., that light falling into the early subjective day might induce testicular regression, provided that no light falls into the subjective night as well. Investigations of such a possibility seem promising.

Acknowledgements

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Hypothalamic and Extrahypothalamic Brain Centers Involved in the Control of Circadian and Circannual Photoneuroendocrine Mechanisms

H. G. Hartwig

Most living organisms exhibit endogenous daily and annual rhythms of metabolic and reproductive functions. In higher vertebrates a part of the prosencephalon, the diencephalon, characterized by its unique combination of photoreceptor cells and secretory active neurons, plays a central role in the integration of extrinsic and intrinsic information necessary for the synchronization of endogenous periodicities with daily and annual changes in the environmental conditions.

In the following presentation characteristic morphological features of brain centers and their afferent and efferent connections involved in the control of circadian and circannual rhythms in birds will be briefly summarized. From a comparative point of view attention will be focussed on brain centers triggering rhythmic autonomous functions in mammals.

Diencephalon

Disturbances of circadian and circannual functions induced by surgical lesions indicate that two major components of the diencephalon, the epithalamic pineal organ and the phylogenetically old periventricular and medial hypothalamus, are closely related to the control of endogenous rhythms.

Hypothalamus

The morphological and functional integrity of the hypothalamo-hypophysial system is a necessity for the central nervous control of endogenous periodicities. Hypothalamic neurons synthesizing, releasing or inhibiting hormones send their axon terminals to the neurohemal contact area (palisade layer) of the median eminence. These secretory active neurons build up the final neuroendocrine pathway triggering the rhythmic secretory activity of the adenohypophysis and consequently the activity changes of the peripheral endocrine system via a phasic release of neuropeptides into specialized portal hypophyseal capillaries.

The observation of unevenly distributed cytoarchitectonic parameters such as size and density of neurons led neuroanatomists to the description of circumscribed hypothalamic nuclei. Recent immunocytochemical, surgical and electrophysiological results demonstrated that these classical hypothalamic nuclei only to a rather limited extent represent functional subunits of the hypothalamus (for review, see Oksche & Farner, 1974; Oksche, 1978). From a functional point of view the parvocellular hypothalamus can be divided into two major subunits closely interconnected by neuronal circuits: the posterior hypothalamic area (tuberal nuclei and median eminence) and the anterior hypothalamus including the preoptic region (see Fig. 1). The parvocellular anterior and posterior hypothalamus both contain a mosaic-like pattern of neuronal clusters com-

Zentrum für Anatomie und Cytobiologie, Justus Liebig-Universität, D-6300 Gießen, Bundesrepublik Deutschland

posed of secretory active and conventional nerve cells. These clusters are surrounded by areas of neuropil rich in specific synaptic profiles. They might represent functional subunits of the parvocellular hypothalamus (for further details and review, see OKSCHE 1978 and 1980).

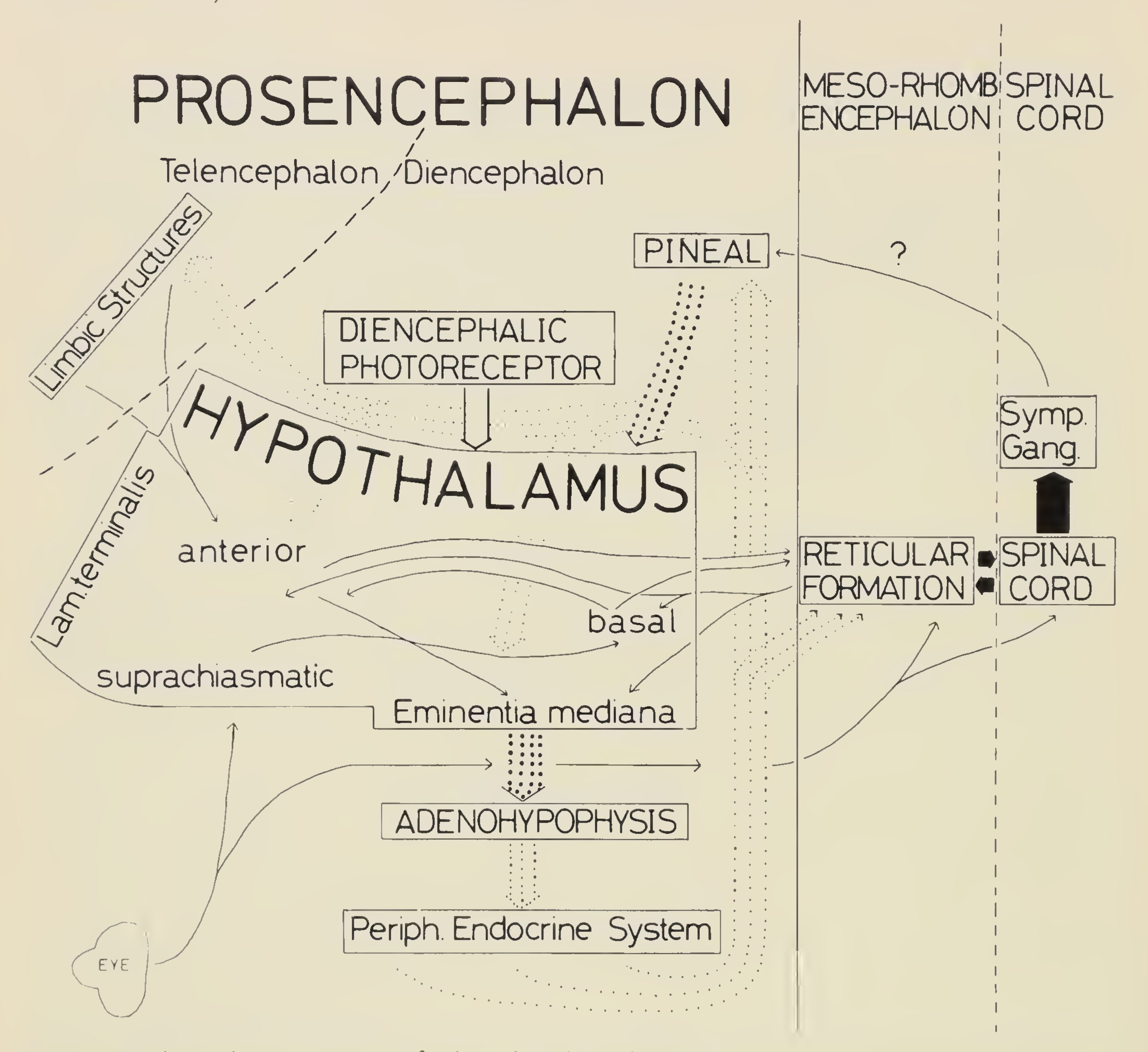


FIGURE 1 Schematic presentation of selected, well established inputs and outputs to rhythmogenic brain areas (pineal organ and phylogenetically old periventricular and medial anterior hypothalamic region).
Arrows: neuronal mono- or multisynaptic pathways; large dots: neuro-humoral, and small dots: humoral circulation; for further details, see text.

In mammals and birds the surgically deafferented posterior hypothalamus maintains a basal neuroendocrine activity preventing complete involution of peripheral endocrine glands. However, the completely isolated posterior hypothalamus does not appear capable of integrating extrinsic and intrinsic information necessary for synchronizing rhythmic autonomic functions with changes in environmental conditions. Lesions of afferents entering the basal (posterior) hypothalamus from an anterior direction interrupt time-dependent neuroendocrine events (e.g. ovulation; for review, see FOLLETT & DAVIES, 1975). Apparently the periventricular and medial anterior hypothalamus contains an important nervous center controlling (or coupling?) circadian and most prob-

ably also circannual neuroendocrine events. In laboratory rodents the suprachiasmatic nuclei located dorsal to the optic chiasma are thought to generate circadian rhythms (for review, see RUSAK, 1977; for the lateral hypothalamic control of autonomic rhythms in mammals, see ROWLAND,1976). In birds the morphological delineation of the suprachiasmatic nucleus is more difficult than in mammals. However, in birds and in mammals the suprachiasmatic nucleus is the exclusive hypothalamic area receiving a direct retinal input (for review, see BONS, 1976; HARTWIG, 1974).

In addition to the direct retino-hypothalamic connection there exist other accessory retinal afferents directed to extrahypothalamic autonomic brain areas (e.g. multisynaptic pathways to the mesorhombencephalic reticular formation and to sympathetic ganglia; for review, see CONRAD & STUMPF, 1975). However, circadian and circannual photoneuroendocrine mechanisms in birds do not depend on the functional integrity of the visual system. Birds and lower vertebrates possess a directly photosensitive diencephalon. At least in the House Sparrow the eyes do not participate in the photoperiodic photoreception controlling seasonal gonadal activities (MENAKER and coworkers, see MCMILLAN et al., 1975). Several investigators attempted to localize the site of extraretinal diencephalic photosensitivity by implanting pieces of radioluminescent material or light conducting optic fibers into various hypothalamic and extrahypothalamic brain regions (for review, see YOKOYAMA et al., 1978). According to the findings of Yokoyama et al. (1978) in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii,* "the diencephalic photoreceptors must lie either within the ventromedial hypothalamus or in sites ventral thereto such as the tuberal complex". This assumption is in agreement with the observation that in the Japanese Quail the deafferented basal hypothalamus is capable of mediating light-dependent gonadal growth induced by local implants of radio-luminescent material (OLIVER et al., 1977).

Neither the exact anatomical location nor the afferent and efferent connections or the structure of extraretinal diencephalic light receptors are known. MCMILLAN et al. (1975) have shown that in the House Sparrow diencephalic light receptors can be stimulated by an extremely low intensity of experimental illumination (0.15 erg/cm^2 for λ = 600—700 nm). Only about 10^{-5} % of photons (λ = 600—700 nm) penetrate through the intact skull down into the tuberal hypothalamus (HARTWIG & VAN VEEN, 1978). Under the view of these data the energy values of MCMILLAN et al. (1975) can be calculated as photons/sec reaching the tuberal hypothalamus. This value is in the range of the sensitivity threshold of the dark adapted retina. Since photopigments are kown to be the most light sensitive compounds in vertebrates, one might conclude that diencephalic photoreceptors contain photopigments (for other possible candidates such as carotenoid chromophores, light sensitive enzymes, see HARTWIG, 1975). Microspectrophotometric recordings (HARTWIG, 1975; see also OKSCHE & HARTWIG, 1975) in 30—50 µm frozen brain sections of small individuals of fish *(Phoxinus phoxinus, Salmo gairdneri, Carassius auratus)* and frog tadpoles *(Rana temporaria)* demonstrated that a hypependymal area located rostral to the paraventricular organ contains a photolabile compound (absorption maximum: 560 to 580 nm; specific density of 0.0057—0.0114 E/µm at λ_{max}). Microspectrophotometric recordings in larger individuals of the same species of fish as well as investigations in brain slices of the House Sparrow failed to detect this substance (due to technical and physical limitations, see HARTWIG, 1975). In *Phoxinus phoxinus* and in tadpoles of *Rana temporaria* this conspicuous area located

at the borderline between hypothalamus and thalamus is rich in bulbous cilia of the sensory type ($9 \times 2 + 0$) projecting into the cerebrospinal fluid (Oksche & Hartwig, 1975). These bulbous cilia closely resemble outer segments of early developmental stages of retinal photoreceptor cells.

Diencephalic photoreceptors analyze the intensity of environmental light. The measured light intensity values are correlated to the signals of the enigmatic "master clock". Thus, diencephalic extraretinal photoreceptors are not concerned with visual functions. Visual photoreceptor cells depend on a high local concentration of photopigments (lamellated outer segments). Light intensities could easily be measured by a large number of scattered low-sensitive elements interconnected by an integrating apparatus. The observed bulbous cilia might be a morphological correlate of the deep diencephalic photoreceptor.

Only the neuroepithelial matrix of the diencephalic primordium is capable of forming photoreceptor cells. Sacerdote (1971) in lesion experiments in adult crested newts, *Triturus cristatus,* inserted methylene blue-soaked barriers at the level of the rostral median eminence. This barrier induced the differentiation of ectopic retinal structures in the basal hypothalamus indicating the potential capacity of the tuberal hypothalamus to develop photoreceptors. Sacerdote's observation provides further evidence for the assumption that extraretinal diencephalic photoreceptors must be located in the ventromedial hypothalamus or in the tuberal area.

Pineal organ

The pineal organ develops as a sac-like evagination of the dorsal diencephalic roof. In birds three major morphological types of pineal organs (saccular in House Sparrow; tubulofollicular in pigeon and duck; lobular in fowl) can be differentiated. Electrophysiological recordings of pineal multiple unit activity in various avian species failed to demonstrate a direct pineal photosensitivity which is well established in pineal organs of lower vertebrates (for review, see Menaker & Oksche, 1974). In the House Sparrow and in other avian species the pineal organ is connected to other brain areas via a pineal stalk containing a bundle of unmyelinated nerve fibers. Interruption of the pineal stalk fibers apparently does not interfere with rhythmic pineal functions (see below). The pineal organ synthesizes indolamines (predominantly serotonin and melatonin). The rate of indolamine synthesis depends on the light perceived in retinal photoreceptor cells and on various hormonal factors (for review, see Ralph et al., 1975; Preslock, 1976). In mammals, photic information is mediated to the pineal organ via the sympathetic superior cervical ganglion. In contrast to the situation in mammals, apparently in the Quail the superior cervical ganglion is not involved in the transmission of retinally perceived light impulses (Herbuté & Baylé, 1976).

The secretory activity of the pineal organ modulates circadian and circannual photoneuroendocrine responses. It is important to note that the resulting autonomic effects of pineal secretory products depend on the actual metabolic and hormonal situation of the analyzed specimen (Balemans, 1972).

Pinealectomy in the House Sparrow results in a loss of circadian rhythmicity. Transplantation of pineal tissue into the anterior eye chamber restores circadian rhythmicity (Zimmerman, 1976). Thus, the pineal acts as a neurosecretory organ and not via neu-

ronal spikes transmitted through the pineal stalk fibers. In this respect it is interesting that the blood-brain barrier is not present in the pineal organ of the House Sparrow (HARTWIG, unpublished results of long-period i.p. application of trypan blue).

Pinealectomy in European Starlings did not interrupt circadian activity rhythms in all individuals investigated (GWINNER, 1977). Future experiments (e.g. rhythmic application of pineal secretory products) may be helpful in elucidating the question whether the pineal functions as a self-sustaining circadian oscillator or whether pineal hormonal signals act as a coupling agent for various central nervous oscillators (for details, see GWINNER, 1980). It should be noted that the contradictory results of pinealectomy in the House Sparrow and in the European Starling might depend on the fact that indolamines synthesized in the pineal organ have also been found in other sites of brain tissue (e.g. retinal melatonin).

Extradiencephalic inputs to the hypothalamus

Daily and seasonal changes of environmental illumination perceived by extraretinal diencephalic photoreceptors are the most important environmental input to hypothalamic oscillating systems. However, it is well established that a large quantity of additional extradiencephalic afferents modulate the light-dependent response pattern. Inputs to the hypothalamus may be classified as a) humoral and b) neuronal. Only a limited number of these inputs have been analyzed in detail. In the following attention will be focussed as an exemplitory excurse to three autonomic inputs to the hypothalamohypophysial system: 1) sex steroid level, 2) ascending monoamine system of the reticular formation, and 3) telencephalic effects on rhythmic neuroendocrine events.

Sex steroid hormones

In birds as well as in other vertebrates a considerable number of periventricular and medial anterior hypothalamic and tuberal neurons take up sex steroid hormones in a receptor-like manner. "Sex steroid hormone retention may be the first step in the modulation of neuroendocrine events and sex behavior" (MORRELL et al., 1975). The anterior hypothalamic steroid binding neurons are located in a hypothalamic area characterized by the presence of LH-RH producing perikarya (duck and Quail: BLÄHSER, 1977; duck: BONS et al., 1978). However, it remains to be elucidated whether LH-RH synthesis and sex steroid binding sites occur in one and the same individual neuron (for the puzzling problem that LH-RH producing neurons are located outside the tuberal hypothalamus, which itself functions as a LH-RH releasing center, see OKSCHE, 1978; for general considerations of structural and functional properties of peptidergic neurons, see SCHARRER, 1978).

Reticular formation of the meso-rhombencephalon

In mammals and birds there exist close neuroanatomical interconnections between the reticular formation of the lower brain stem and the hypothalamus. Best analyzed are the morphological and functional properties of the ascending monoamine pathways. In mammals and birds monoamine perikarya of the reticular formation project to the anterior and posterior hypothalamus including the median eminence (for references, see CALAS et al., 1974). In mammals it is well established that ascending catechol-

amine perikarya modulate hypothalamic neuroendocrine events (cf. WUTTKE et al., 1977), whereas the ascending serotonin fiber system is engaged in the control of sleep-wakefulness cycles (KIIAUMAA & FUXE, 1977). Recently, a delicate indolamine fluorescence has been found in the suprachiasmatic area of the Quail (HARTWIG, unpublished). However, the input of serotonin afferents to the suprachiasmatic nucleus in mammals is not critical for the generation of circadian rhythmicity (BLOCK & ZUCKER, 1977). In the duck and in the Quail noradrenaline (NA) perikarya have been localized in the *Locus coeruleus,* and serotonin (5HT) perikarya have been identified in the raphe nuclei (unpublished results; duck: BONS, CALAS & HARTWIG; Quail: HARTWIG). In the duck, the House Sparrow and in the Quail, periventricular and medial hypothalamic areas are rich in a dense network of NA terminals and preterminals. A similar high concentration of NA terminals and preterminals exists in the internal zone of the median eminence, whereas only a small number of dopamine—and serotonin—containing fluorescent elements has been identified in the palisade layer of the median eminence. It should be noted that birds and lower vertebrates in contrast to mammals do not possess a tuberal dopamine neuron system projecting to the palisade layer of the median eminence. In the Japanese Quail hypothalamic deafferentation results in a dramatic decrease of fluorescent structures indicating their extrahypothalamic origin (exception: paraventricular organ; NOZAKI & KOBAYASHI, 1975). In the Quail and in the pigeon it has been shown that ascending monoamine pathways are engaged in the control of circadian and circannual neuroendocrine events (Quail: NA control of ovulation, CAMPBELL & WOLFSON, 1974; pigeon: control of stress-induced corticosterone rise by raphe nuclei, MAURIN et al., 1977).

In summary, the ascending monoamine fiber systems project to phylogenetically old periventricular and medial hypothalamic areas. These areas are formed by neuronal cell clusters exhibiting a patternlike arrangement. Future investigations should deal with the analysis of these cell patterns and their afferent fiber systems (see OKSCHE, 1978).

Telencephalic effects on periodic autonomic functions

In birds telencephalic effects on periodic autonomic functions have not been studied in detail (for references and effects of telencephalic stimulation on ovulation, see JUHASZ & VAN TIENHOVEN, 1964). In mammals telencephalic and limbic projections to the anterior hypothalamic region and to the reticular formation of the lower brain stem are well established. One should bear in mind that circadian oscillations might occur not only in diencephalic neuronal systems (e.g. circadian rhythm of synaptic excitability in rat and monkey hippocampal granule cells, see BARNES et al., 1977).

Summary and conclusion

The schematic presentation in Fig. 1 deals with the neuronal and humoral afferent and efferent connections of dienephalic brain centers engaged in the control of rhythmic autonomic functions in birds. The secretory active pineal organ and phylogenetically old periventricular and medial areas of the anterior hypothalamus formed by interconnected clusters of neurons seem to be the major central nervous components controlling (driving or coupling?) endogenous rhythmic activities of the tuberal hypo-

thalamus. Neuroendocrine activities of the tuberal hypothalamus trigger via the adenohypophysis periodic peripheral metabolic and endocrine functions. Extraretinal and extrapineal diencephalic photoreceptors perceive environmental light cues and synchronize via unknown neuronal (or neurohumoral?) mechanisms endogenous rhythmicity with daily and seasonal changes in the environmental conditions.

In Fig. 1 only selected and well established neuronal and humoral inputs and outputs of rhythmogenic brain areas are shown. Nevertheless, the scheme is of a striking complexity. It is easily conceivable, that such a complex pattern of neuronal and humoral feedback circuits could contain more than one self-sustaining oscillating mechanism. According to FARNER et al. (1977) "photoperiodic control systems in birds are of quite recent and very probably of multiple origin". Thus, it would not be surprising to find differences in the location and functional properties of brain centers supervising photoperiodic mechanisms. Moreover, it should be noted that contradictory results from similar experimental approaches might be based on the fact that in the course of recovery of experimentally induced disturbances the central nervous system constructs new and independent self-sustaining oscillating neuronal circuits. In intact and experimental animals the coupling of multiple oscillating centers might depend on various individual parameters such as age, hormone levels and actual metabolic situation.

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On the Organization of Avian Circadian Systems: The Role of the Pineal and Suprachiasmatic Nuclei

JOSEPH S. TAKAHASHI and MICHAEL MENAKER

Introduction

The enterprise of attempting to understand the physiological mechanisms that underlie the generation and control of circadian rhythms in multicellular organisms is at an exciting and propitious stage (for review, see MENAKER et al., 1978). Although thirty years ago KRAMER's (1950) demonstration of sun compass orientation in Starlings implied that birds possess internal biological clocks, progress in unravelling the physiological mechanisms of circadian rhythmicity in birds has been slow. However, since the initial demonstration that House Sparrows *(Passer domesticus)* synchronized their circadian activity to light-dark cycles without their eyes, steady progress has been made in locating some of the major components of the "circadian system" in this species. We are now in a position to say that certain organs and groups of cells in the Sparrow brain contain components crucial for the integration of circadian rhythmicity at an organismal level. In this paper we review what is currently known about the physiology of the circadian system of the House Sparrow. Although the "system" appears complex, we feel it is tractable and open to experimental analysis at both organismal and subcellular levels.

We have divided the paper into sections which focus upon different aspects of the Sparrow circadian system. Since lighting information is the most important input to the circadian system, we first describe the photoreceptors that mediate the various effects of light. Then we consider two neural structures, the pineal and the suprachiasmatic nuclei, which are required for the persistence of circadian rhythmicity in sparrows. The subsequent sections focus upon experiments that were designed to determine whether or not the pineal gland is the pacemaker which drives the circadian system of the House Sparrow. Finally, we present evidence that the pineal is indeed a circadian oscillator by virtue of the demonstration of the biochemical rhythm in isolated pineals that persists in vitro. In the discussion we have tried to summarize what we know about avian circadian systems and to speculate on their general organization.

Photoreceptors for entrainment

In the House Sparrow both retinal and extraretinal photoreceptors mediate entrainment of circadian activity rhythms to light-dark cycles. The locomotor rhythms of enucleated House Sparrows can be synchronized by ambient light cycles of very low intensity (MENAKER, 1968). In addition, light perceived extraretinally affects the free-running periods of the rhythms of birds exposed to different intensities of constant light (ASCHOFF's Rule) and also contributes to the production of arrhythmic activity by high intensities of constant light. The extraretinal photoreceptors mediating these three responses are located within the brain of the Sparrow (MENAKER, 1971; MCMILLAN et al., 1975 a, b, c). Recent experiments using fiber optics to illuminate discrete regions of

Department of Zoology, University of Texas, Austin, Texas 78712, U.S.A.

the brain indicate that the photoreceptors may be localized and perhaps numerous (MENAKER et al., unpublished results).

The eyes (presumably the retinae) of House Sparrows also mediate effects of light that contribute to the three circadian parameters already described. The eyes and extraretinal photoreceptors are additive in their interaction. In the case of arrhythmicity induced by constant light, the eyes are necessary in order to achieve arrhythmicity (MCMILLAN et al., 1975 a, b, c).

Effects of pinealectomy

Searching for the extraretinal photoreceptors that entrain activity rhythms in Sparrows, GASTON & MENAKER (1968) removed pineal glands from blind Sparrows entrained to light-dark cycles and found that entrainment to light persisted. This established that if the avian pineal is photoreceptive, it is not the sole brain photoreceptor because entrainment occurs in the absence of both the eyes and the pineal.

Although the pineal is not required for entrainment, its removal has dramatic effects on the persistence of circadian rhythmicity in constant darkness (Fig. 1a). In constant conditions pinealectomy abolishes free-running rhythmicity in House Sparrows (GASTON & MENAKER, 1968; BINKLEY et al., 1971). Spectral analysis of the activity records indicates that pinealectomized Sparrows are indeed arrhythmic and do not show residual ultradian periodicities. Within broad limits, the quantity of activity is not changed by pinealectomy but rather is evenly distributed with respect to time (BINKLEY et al., 1972). When birds are entrained to light cycles before they are released into constant darkness, arrhythmicity is attained gradually over many cycles during which the duration of the active portion lengthens until continuous activity occurs (Fig. 1b). For LD 8 : 16 light cycles, the mean number of cycles before arrhythmicity is 8.1 ± 2.8 cycles ($\bar{x} \pm$ S. D., N = 15). When pinealectomy is performed in constant darkness, the mean number of cycles before arrhythmicity is reduced to 5.3 ± 5.4 cycles ($\bar{x} \pm$ S. D., N = 19) (from GASTON, 1969).

In certain light cycles, especially ones with short light portions or with a period length greater than 24 hours, the activity onset of Sparrows precedes the onset of light. This "phase lead" of the activity rhythm reflects the entrainment behavior of endogeneous circadian oscillators (ASCHOFF, 1960). In pinealectomized Sparrows on light — dark cycles the phase lead of the activity rhythm persists (Fig. 1b) and on the average is increased (GASTON, 1971).

In constant environmental conditions the pineal is crucial for the persistence of free-running rhythmicity. Thus pineal removal abolishes the feature which is the most important criterion for the existence of a circadian rhythm — its self-sustained free-running oscillation. Whether or not the abolition of this feature of circadian rhythms justifies the conclusion that the pineal is the "clock" will be discussed later. Whatever role the pineal gland plays in the Sparrow, it is clear that the pineal cannot contain the entire circadian system because Sparrows can synchronize to light cycles without their pineals. Since the activity of pinealectomized Sparrows appears to be entrained rather than directly driven by light cycles and since the activity rhythm gradually decays in constant darkness, it has been proposed that in addition to the pineal gland there is a "damped" oscillator which has access to environmental light and which directly drives

locomotor activity (GASTON & MENAKER, 1968; MENAKER & ZIMMERMAN, 1976). An alternative to this model is that there are multiple oscillators, located outside the pineal, which have photoreceptive input and are entrained or driven by the pineal gland. Under normal conditions the pineal would serve to "couple" these oscillators so that they maintain cohesive phase relationships to one another and behave synchronously as a unit. The arhythmia of pinealectomized Sparrows in constant conditions would then result from the constituent oscillators free-running and drifting out of phase with one another (GASTON & MENAKER, 1968; GWINNER, 1978).

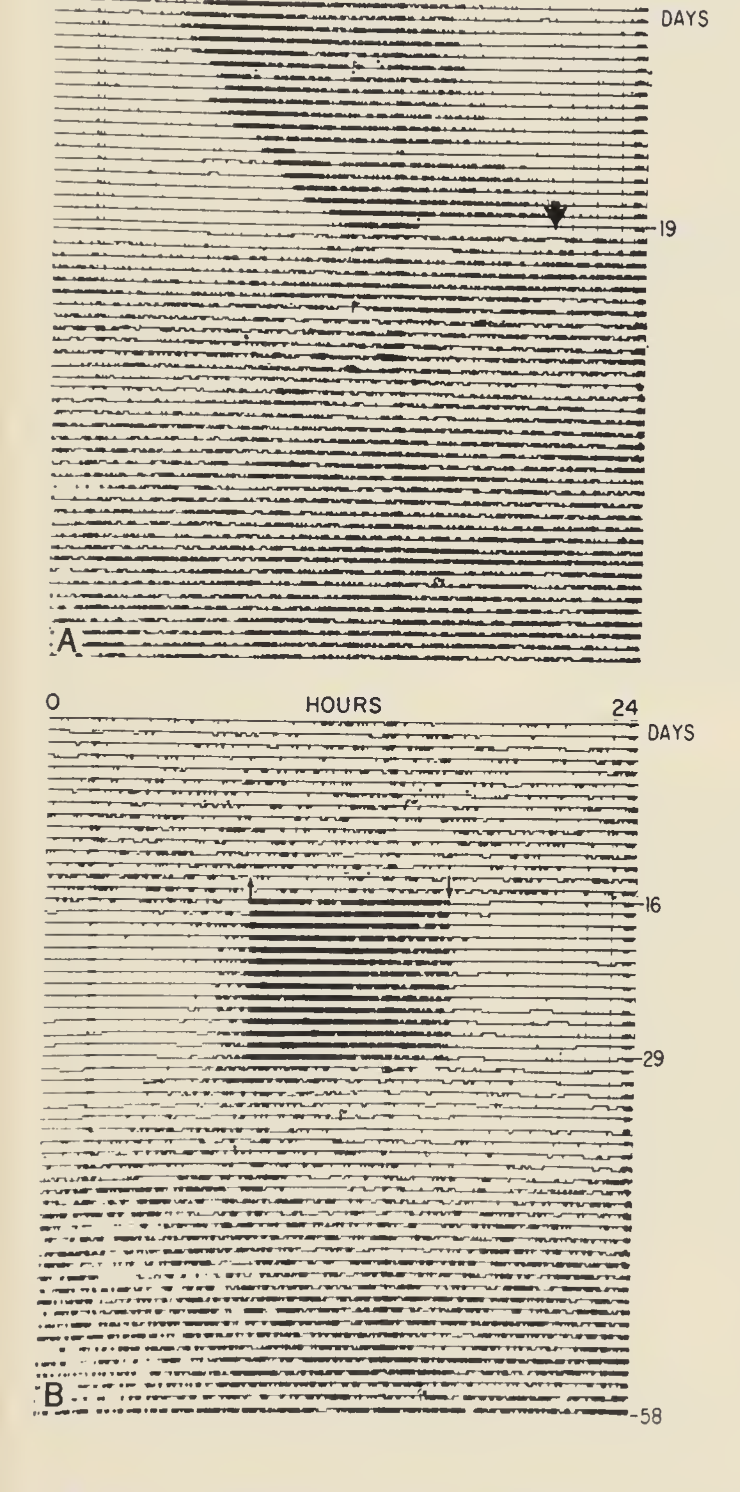


FIGURE 1. The effect of pineal removal on the activity of House Sparrows. Each horizontal line represents the activity record during a 24-hour interval. The record is continuous: each successive day is below the previous one with time progressing from left to right and top to bottom. The bird is active where the record is dense. (A) An example of a sparrow which was pinealectomized while free-running in constant darkness. The operation was performed on day 19, indicated by the arrow. (B) The entrainment of a pinealectomized sparrow. The bird was in constant darkness until day 16 when a LD 8 : 16 light cycle (indicated by the arrows) was initiated. On day 29, the sparrow was transferred to constant darkness. (from GASTON & MENAKER, 1968).

Recent eyperiments indicate that the latter explanation of the behavior of pinealectomized sparrows is more plausible. Pinealectomized sparrows exhibit abnormal activity patterns in certain light cycles which have an interrupted light portion (i.e., "skeleton" light cycles). The behavior of House Sparrows has been extensively studied in

such skeleton light cycles and the results strongly suggest that the behavior of pinealectomized Sparrows reflects the behavior of a population of oscillators located outside the pineal (TAKAHASHI, et al., unpublished results).

Role of the suprachiasmatic nuclei

In mammals, lesions that destroy the suprachiasmatic nuclei of the hypothalamus abolish a variety of circadian rhythms and disrupt entrainment to light-dark cycles. Suprachiasmatic lesions have been shown to eliminate free-running circadian rhythms in a variety of rodents and in one primate. These results have been generally interpreted as evidence that the suprachiasmatic nuclei act as a circadian pacemaker in the mammalian circadian system (MENAKER et al., 1978; MOORE, 1978, for reviews).



FIGURE 2. The effect of suprachiasmatic lesions on the activity of House Sparrows. This figure is "double plotted" so that each horizontal line is 48 hours in duration. (A) Effect of a lesion on circadian activity in constant darkness. The operation was performed at the time indicated by the arrow. (B) Entrainment of a lesioned sparrow. The bird is in a LD 12 : 12 light cycle (indicated by the small arrows) for 15 days. The heavy arrow on the right hand side of the figure indicates when bird was transferred to constant darkness. (from TAKAHASHI & MENAKER, in preparation).

In the House Sparrow, the avian "homologue" of the mammalian suprachiasmatic nucleus has been described by CROSBY & WOODBURNE (1940). Additionally, HARTWIG (1974) has reported a direct retinal projection to the contralateral suprachiasmatic nucleus in *Passer.* In view of the anatomical similarities of the suprachiasmatic nuclei in birds and mammals, we speculated that functional similarities might also exist. We were particularly interested in the possibility that the suprachiasmatic nuclei might contain the oscillator(s) located outside the pineal gland.

Figure 2 a shows the effect of a lesion that destroyed both the suprachiasmatic nuclei (Takahashi & Menaker, in prepararion). Notice that the free-running activity rhythm eypressed before the lesion is severely disrupted after supraciasmatic ablation. This result is representative of ten sparrows which sustained lesions bilaterally destroying at least 80 % of the suprachiasmatic nuclei. Spectral analysis of the activity records of these birds indicates that the activity is arrhythmic. Unlike hamsters bearing suprachiasmatic lesions (Rusak, 1977), sparrows with such lesions rarely express residual ultradian periodicities in their activity. Lesions that spared the suprachiasmatic nuclei were completely ineffective in eliminating free-running circadian rhythmicity. Partial lesions or unilateral suprachiasmatic lesions also did not abolish rhythmicity; although in some cases there is evidence for unstable rhythms.

When sparrows that are arrhythmic as a result of suprachiasmatic lesions, are exposed to light-dark cycles, they express rhythmic activity patterns (Fig. 2 b). Since the activity onset precedes the onset of the light portion in some light cycles and since the activity rhythm appears to "damp" out when sparrows are transferred from a light cycle to constant darkness, it appears that suprachiasmatic lesioned sparrows retain the ability to entrain to light cycles. Thus, to a first approximation the results of suprachiasmatic lesions are indentical to those of pinealectomy in *Passer*. Both surgical procedures abolish free-running rhythmicity in constant darkness, but do not abolish entrainment to light dark cycles. These results raise two sets of questions concerning the organization of the circadian system of the House Sparrow. First, what is the relative importance of the pineal gland and the suprachiasmatic nuclei in generating circadian rhythms in birds and how do they interact? Second, are the avian pineal and suprachiasmatic nuclei autonomous circadian oscillators? The sections that follow attempt to address these questions.

Neural connections of the pineal

In mammals, the pineal must receive an intact innervation from the suprachiasmatic nuclei in order to express circadian rhythmicity. Interference with the neural pathways from the suprachiasmatic nuclei to the pineal, which include fibers whose cell bodies lie in the superior cervical ganglia, results in the elimination of the rhythm of pineal N-acetyltransferase activity (Moore & Klein, 1974).

In sparrows, the pineal also receives sympathetic input from fibers originating in the superior vervical ganglia. The only known neural output from the pineal is a set of unmyelinated, acetylcholinesterase-positive fibers which leave the pineal ventrally through its stalk. In order to determine whether the known neural inputs or outputs of the pineal were necessary to sustain circadian rhythmicity, Zimmerman & Menaker (1975) attempted to isolate the pineal from its neural connections. Neither surgical interruption of the fibers leaving the pineal stalk nor chemical sympathectomy with systemic 6-hydrocydopamine injections nor both procedures together eliminated free-running circadian rhythmicity. This demonstrates that neural connections are not necessary for the Sparrow pineal to function within the circadian system and that, unlike the mammalian pineal, the avian pineal may not require neural input from the suprachiasmatic nuclei. Since neural coupling is not necessary, Zimmerman & Menaker (1975) proposed that the pineal was hormonally coupled to the rest of the circadian system.

Pineal transplantation

If the pineal is hormonally coupled to the circadian system, then it should be possible to restore rhythmicity in an arrhythmic pinealectomized sparrow by transplanting the pineal of a donor bird. GASTON (1971) first reported limited but tantalizing success in this endeavor. Only some years later were ZIMMERMAN & MENAKER (1975) able to transplant pineals successfully on a regular basis. Figure 3 illustrates the result of transplanting the pineal gland from a donor bird into the anterior chamber of the eye of an arhythmic pinealectomized recepient. Pineal transplantation unambiguously restores circadian rhythmicity in pinealextomized sparrows (ZIMMERMAN & MENAKER, 1975;



FIGURE 3. The effect of pineal transplantation on the activity of a pinealectomized sparrow in constant darkness. A pineal from a donor bird was transplanted into the anterior chamber of the eye of the recipient on the day indicated by the arrow. (from ZIMMERMAN & MENAKER, 1976).

MENAKER & ZIMMERMAN, 1976). Note that rhythmicity is apparent within one or two days after transplantation making it unlikely that sympathetic reinnervation from the iris is necessary. These results strongly suggest that the pineal is indeed hormonally coupled (at least on its output side) to the rest of the circadian system.

The result of restoring rhythmicity by pineal transplantation, however, does not allow us to discriminate between two possible interpretations of the pineal's role in the circadian system of the sparrow. The first and more interesting interpretation is that the pineal is the pacemaker which drives the circadian system. The second interpretation is that the pineal plays a permissive role, allowing the expression of circadian rhythmicity generated by a pacemaker located elsewhere. In order to discriminate between these alternatives, it is necessary to demonstrate that, in addition to restoring rhythmicity, pineal transplantation transfers some property of the pacemaker. ZIMMERMAN & MENAKER (MS submitted) tested this proposition by attempting to transplant the phase of the rhythm of the donor bird. They found that the phase of the restored rhythm was closely related to the phase of the donor bird and was not randomly distributed nor correlated with the time of surgery. Thus, this experiment strongly supports the hypothesis that the pineal is a pacemaker within the Sparrow circadian system.

Effects of melatonin

Since the pineal organ appears to be hormonally coupled on its output side to the rest of the circadian system of the House Sparrow, a likely candidate for this role is melatonin, an indoleamine which is actively synthesized in pineals. Melatonin exhibits a circadian rhythm in both pineal content and serum levels (RALPH et al., 1974). Pineal melatonin thus could act at sites remote from the pineal. As a first step in addressing the question of whether melatonin is involved, TUREK et al. (1976) implanted intact sparrows with chronic doses of melatonin. They found that low doses of melatonin shorten the free-running period lengths of the activity rhythms and that high doses induce continuous activity that approaches arrhythmicity. These data support the notion that melatonin is involved in the control of circadian locomotor rhythmicity; however, they do not demonstrate how exogenous melatonin acts nor what role endogenous melatonin plays.

Biochemistry of the pineal gland: Rhythmicity in vitro

A great deal is known about the biochemistry of the mammalian pineal (AXELROD, 1974; AXELROD & ZATZ, 1977, for reviews). The synthesis of melatonin appears to be regulated by the activity of the enzyme, N-acetyltransferase. In rats, the activity of this enzyme exhibits a spectacular circadian rhythm giving rise to a 50-fold increase in enzymatic activity at night. The activity of N-acetyltransferase appears to be regulated by β-adrenergic receptors which are innervated by sympathetic fibers which originate in the superior cervical ganglia (AXELROD & ZATZ, 1977, for review).

In chickens the activity of pineal N-acetyltransferase exhibits a circadian rhythm which persists for at least two cycles in constant darkness (BINKLEY & GELLER, 1975). The control of N-acetyltransferase activity, however, appears to be different in birds and mammals. The activity of pineal N-acetyltransferase appears to be free of sympathetic control in birds (BINKLEY, 1976). In view of these results and those of the pineal transplantation eyperiments, it is possible that the rhythmicity of avian pineals may originate within the gland itself. Indeed this possibility seems correct. BINKLEY et al. (1977) have shown that the timing of the decline in enzyme activity in vitro is related to the light cycle to which the chicks were previously exposed and not to the time the glands were placed into culture. Two other laboratories have now documented a rise and fall in N-acetyltransferase activity in isolated pineals during the first 24 hours in culture (DEGUCHI, 1979; WAINWRIGHT & WAINWRIGHT, MS submitted). KASAL et al. 1979 have demonstrated that the rhythm is indeed circadian, persisting for two cycles in vitro in constant darkness. Thus, the chick pineal is clearly a circadian oscillator.

Discussion

Although we are far from a complete description of the Sparrow circadian system, we can, nevertheless, delineate its major "components". The Sparrow pineal clearly plays a dominant role. The transplant experiments show that the pineal confers phase and periodicity upon the system. The in vitro experiments demonstrate that the chicken pineal is a self-sustained oscillator. It seems reasonable to assume that the Sparrow pineal is also a circadian oscillator and that it is this property of the pineal that enables

the intact circadian system to express self-sustained rhythmicity. Since there is evidence for multiple oscillators located outside the pineal, we propose that the pineal exerts an integrative influence upon these oscillators so that they maintain cohesive phase relationships to one another resulting in the expression of an overt circadian rhythm. Arrhythmicity produced by pinealectomy would, on this model, be the result of "uncoupling" the system, with constituent oscillators free-running and drifting out of phase with one another. Coupling might be maintained by rhythmic output of pineal melatonin or some other pineal product.

The location(s) of the extra-pineal oscillators remains to be determined. It is possible that they are located within the suprachiasmatic nuclei. However, such a conclusion cannot be firmly held at this time because sparrows bearing suprachiasmatic lesions retain their ability to entrain to light cycles. This indicates that there remains at least a damped oscillator which has access to environmental light on its input side and to locomotor activity on its output side. Since lesioned sparrows possessed intact pineal glands it is not clear whether their entrainment behavior is due to the presence of the pineal or the existence of yet a third oscillator (or set of oscillators).

Since sparrows bearing suprachiasmatic lesions are arrhythmic inspite of the presence of the pineal gland, it is clear that neither the suprachiasmatic nuclei nor the pineal maintain the rhythmicity of the bird if the other is removed. At the present time, it seems reasonable to conclude that a pineal-suprachiasmatic complex exerts integrative effects on the Sparrow circadian system.

We have summarized what we know about the organization of the Sparrow circadian system. For comparative reasons, the question of the generality of these results among birds and other vertebrates is of interest. Indeed, the pineal may play a major role in vertebrate circadian systems. Although in mammals, pineal removal has only minor effects on circadian locomotor rhythmicity (QUAY, 1970; KINCL et al., 1970) it is involved in the circadian control of reproduction (ELLIOTT, 1976). Although the pineal of lizards does not appear to be necessary for the expression of rhythmicity, its removal clearly weakens the coupling between at least two oscillatory components which are expressed in lizard activity rhythms (UNDERWOOD, 1977).

Among the birds, pinealectomy abolishes circadian rhythms in *Passer domesticus* (GASTON & MENAKER, 1968), *Zonotrichia leucophrys gambelii* (GASTON, 1971), *Zonotrichia albicollis* (MCMILLAN, 1972) and *Carpodacus mexicanus* (FUCHS & ENRIGHT, personal communication). In Starlings, *Sturnus vulgaris,* pinealectomy severely disrupts circadian rhythmicity; however, only a small percentage of birds become permanently arrhythmic (GWINNER, in press). In chickens, *Gallus gallus,* (MACBRIDE, 1973) and Japanese Quail, *Coturnix coturnix japonica* (SIMPSON & FOLLETT, 1980) pinealectomy has no dramatic effects. Thus, even within the class Aves, the effects of pinealectomy are variable. The lack of effect of pinealectomy in the chicken is particularly puzzling in view of the demonstration that chicken pineals are capable of self-sustained oscillation in vitro. Two factors may be responsible for the variable results of pinealectomy in birds. The experimental conditions under which the various studies were conducted were different. This is especially true of the acoustic environment which could have affected the results either by allowing social entrainment when the white noise background was low or absent, or by actively contributing to uncoupling when the white

noise intensity was high (see Yokoyama, 1980). Alternatively, the variable effects of pinealectomy may be due to true interspecific differences. Such interspecific differences, however, may not be as profound as they first appear to be. If the avian suprachiasmatic nuclei contain selfsustained circadian oscillators, then it is possible that in those species in which coupling among these oscillators is strong, removal of the pineal may be without effect (e.g., chickens, Quail). As Gwinner 1978 has proposed, the Starling may be an intermediate case in which weak coupling exists among the non-pineal (SCN?) oscillators. Thus, pinealectomy in starlings yields intermediate results. In sparrows, it appears that coupling among non-pineal oscillators is extremely weak or nonexistent in the absence of the pineal. In this case pinealectomy leads to complete uncoupling of the remainig oscillators resulting in arhythmicity. Perhaps a single qualitative model of the circadian system of birds is sufficient to explain the effects of pinealectomy if differences in coupling strength among the oscillators that comprise the rest of the circadian system are taken into account.

Acknowledgments

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Investigations on the Possible Roles of the Pineal and the Anterior Hypothalamus in Regulating Circadian Activity Rhythms in Japanese Quail

S. M. Simpson and B. K. Follett

Introduction

Birds possess an elaborate system of circadian rhythms (review, Gwinner, 1975) which are used not only to regulate basic daily functions such as locomotor activity and body temperature but also serve as essential components in sun-compass orientation (review, Hoffmann, 1972) and photoperiodic time-measurement (review, Follett, 1978). How these rhythms are regulated centrally has become an important question and Menaker and his colleagues (Menaker & Zimmerman, 1976) have presented strong evidence for the pineal being a primary oscillator in the House Sparrow, regulating other rhythmic functions via a humoral pathway. In rodents the pineal may not be a driving oscillator but there is much research showing that the suprachiasmatic nucleus is important for the expression of many circadian rhythms (e.g. Rusak, 1977). Our particular interest in the problem arises from various neuroendocrine studies in Japanese Quail which have shown that areas in both the anterior and posterior hypothalamus are vital for photoperiodically induced growth (Davies & Follett, 1975). A number of neural and neuroendocrine functions must be served by these hypothalamic areas, one of which might be associated with the circadian-based photoperiodic clock. Ablation of this clock in Quail can be expected to render the bird incapable of enhancing gonadotrophin secretion when it is exposed to long days (rodents, Rusak & Morin, 1976; Stetson & Watson-Whitmyre, 1976). The possibility, therefore, that the anterior hypothalamus in birds might house a clock cannot be dismissed. Indeed it becomes attractive when it is realised that lesions there not only block gonadal growth but can also stop ovulation — a circadian controlled event (Follett & Davies, 1978) — while anterior hypothalamic deafferentation in pigeons can inhibit the diurnal rhythm in plasma corticosterone (Bouillé et al., 1975).

The present research has sought to ask whether the pineal and/or the anterior hypothalamus are involved in the Quail's circadian system. Since it is not yet possible to monitor the circadian clock(s) involved in photoperiodic time-measurement we have turned to locomotor rhythms as our endpoint. A drawback of Quail is that circadian activity records in this species are less impressive than in perch-hopping species but, despite this, we have continued to use Quail since so much more is known about their neuroendocrinology. It must be emphasised that the results below are only preliminary.

Pinealectomy

The pineal has been removed surgically from 11 sexually immature male Quail and the activity patterns compared with those in 8 sham-operated animals. In all cases records have been collected for two weeks prior to surgery and for 7 weeks thereafter. Histology of the brains at this time indicated no identifiable pineal tissue in 7 of the quail, the other 4 containing small remnants of basal stalk tissue. Overall, no significant

Department of Zoology, The University, Woodland Road, Bristol BS8 1UG, United Kingdom

differences were apparent in the free-running locomotor rhythms of the pinealectomized quail when compared with the controls. Figure 1 shows a typical result: the activity rhythm persisted in DD following pinealectomy (P) and there appears to have been little change in the free-running period (τ), the amount of activity or the activity:rest time. A subjective analysis of all 11 birds suggested that τ was shortened by 10—20 min in 3, lengthened in 3 and unchanged in the remainder. However, in the controls τ was lengthened in 3, shortened in 1 and did not change in the other 4. At the moment, therefore, it is not easy to implicate the Quail's pineal in its circadian locomotor system. A group of six more Quail which hopefully are pinealectomized have been running in various photoperiodic cycles for the past five months: so far none have shown any marked differences from their intact controls.

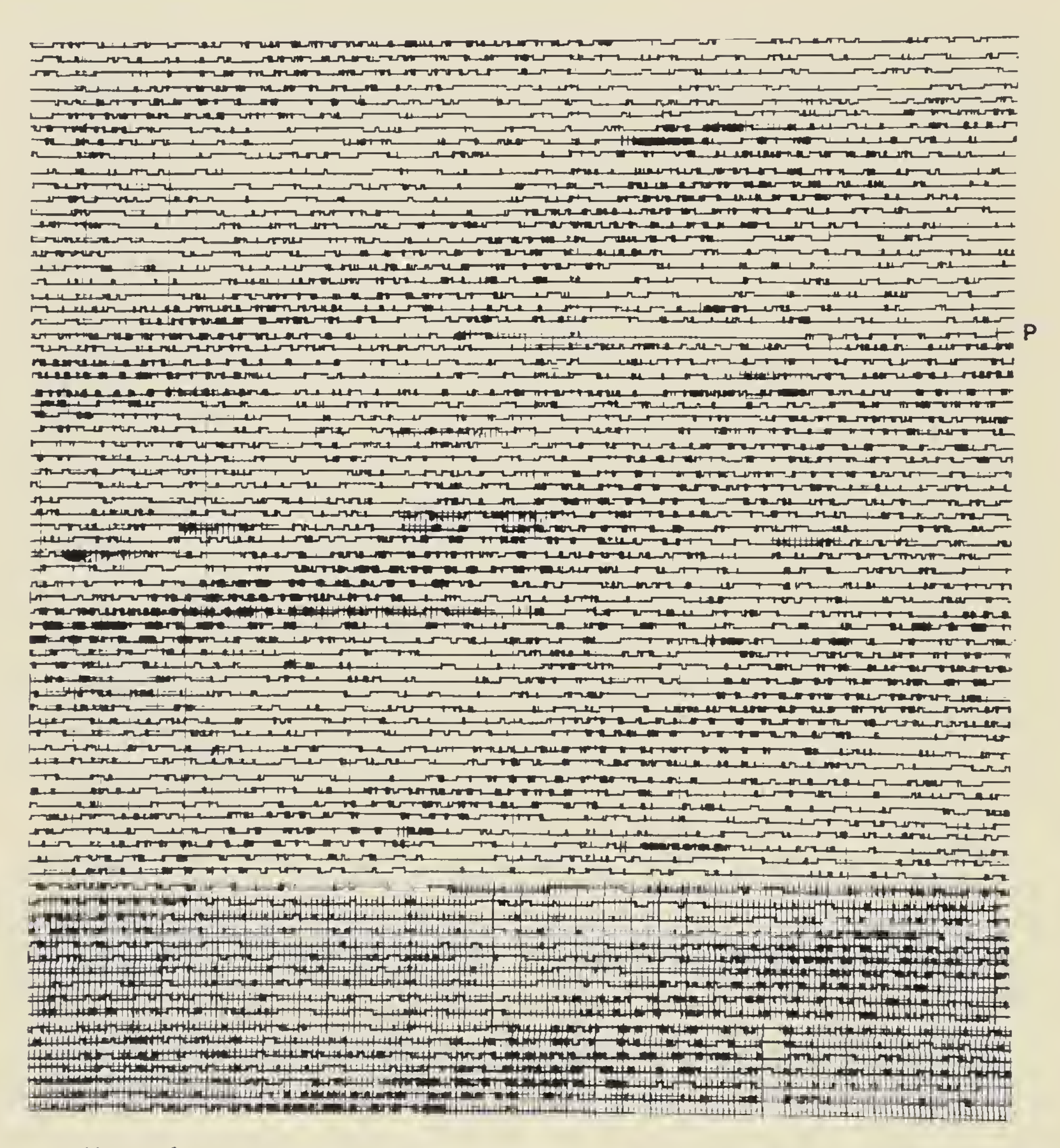


FIGURE 1. The effect of pinealectomy upon the free-running circadian locomotor rhythm in a Japanese Quail held in darkness. The time of pinealectomy is marked with "P". For further details see text.

Melatonin treatment

The elegant experiments of MENAKER & ZIMMERMAN (1976) suggest the pineal influences the Sparrow's circadian system via a humoral pathway and there is supporting evidence from TUREK et al. (1976) that melatonin might be one of the agents involved. They showed that melatonin (given as an i.p. silastic implant) caused either a marked change in τ or a state of continuous activity. In Quail, we have implanted melatonin

capsules s.c. in birds which have been free-running in DD for at least two weeks (2 mm implant n = 7; 20 mm n = 4; 40 mm n = 4). The capsules were left in place for a fortnight and then removed. In every case the overall level of activity was reduced while the implant was in position (Figure 2). Ten of the birds continued to free-run, however, some with small changes in τ which cannot be considered significant since they also occurred in some of eight control birds bearing empty capsules. Five of the melatonin-treated birds showed continuous activity at a low level with the normal circadian pattern being restored once the capsules were removed.

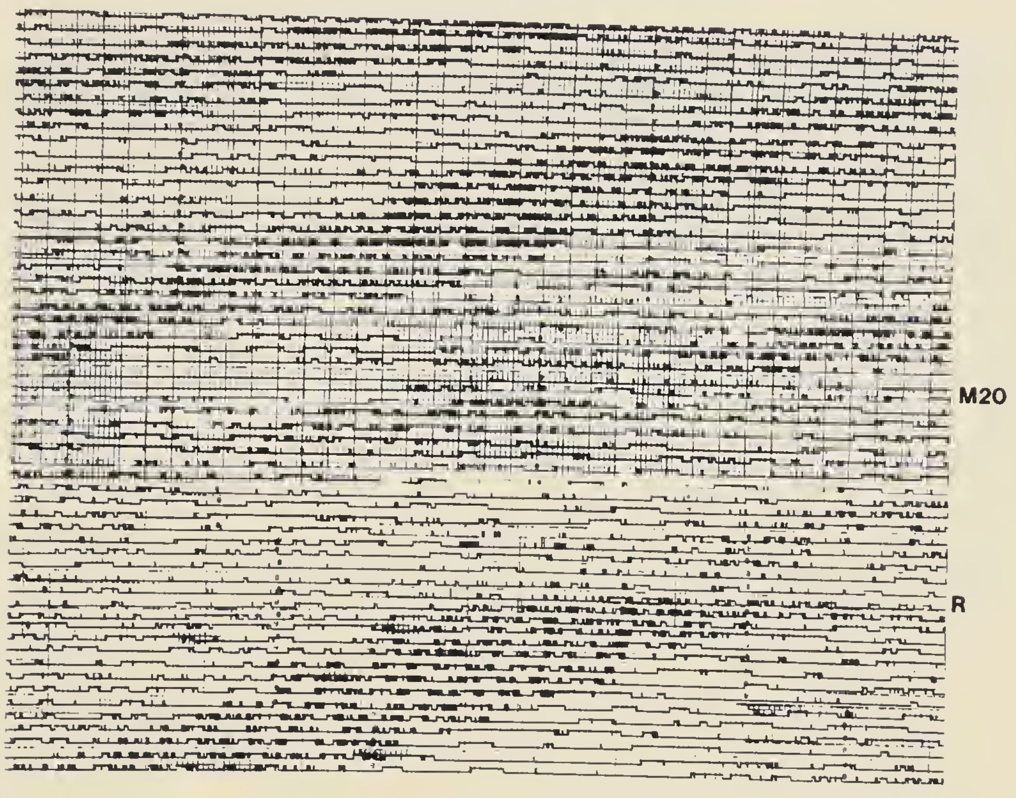


FIGURE 2. The effect of implanting a 20 mm capsule of melatonin (at point M 20), and its subsequent removal (at time R) on the free-running circadian locomotor rhythm in a Japanese Quail.

In another experiment six birds were entrained to 1 L : 23 D that caused a phase lead of activity onset of 4—6 h. Over the next three months each bird received both empty and melatonin-filled implants (20 mm) for periods of between two and four weeks. There was individual variation in the magnitude of the melatonin effects but in all birds a reduction in activity was seen. In some melatonin largely abolished the activity before lights on and reduced it once the lights had gone off. In others it only diminished the phase leading activity but it has not yet been possible to be sure whether the amount of phase lead has been altered.

To a degree, therefore, the results in Quail with melatonin are consistent with those from the pinealectomy experiments — no obvious effects upon the circadian system with the possibility existing that any changes may reflect the pharmacological actions of melatonin in inducing a soporific state. Further experiments are obviously needed but the results so far do raise the possibility that the Quail's pineal may not be as essential to its underlying circadian system as appears to be the case in the House Sparrow. Already, GWINNER (1978) has slightly modified MENAKER's Sparrow model in view of the results which he has obtained with pinealectomized Starlings.

Anterior hypothalamic lesions

So far it has proved possible to induce arrhythmia in four Quail with lesions in the anterior hypothalamus. Autocorrelation analyses showed a circadian periodicity in activity patterns before lesioning and its obliteration thereafter. We are strongly of the opinion that so few birds do not yet allow us to make any firm statement regarding a role for the anterior hypothalamus in the Quail's circadian system, but they are suggestive and deserve being followed up.

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The Possible Role of the Pineal in Photoperiodic Time Measurement in Two Species of Passerine Birds

Katsuhiko Yokoyama

Introduction

Pinealectomy or silastic implantation of melatonin, one of the pineal products, abolishes circadian rhythms of locomotor activity in House Sparrows, *Passer domesticus,* held under constant darkness (Gaston & Menaker, 1968; Turek et al., 1976). Pinealectomy significantly alters patterns of circadian motor activity in European Starlings, *Sturnus vulgaris* (Gwinner, 1978). Experiments involving resonance, skeleton, T-cycle and other experimental photoperiods in several photoperiodic species of birds (Farner, 1975) have demonstrated that photosensitivity of the system controlling gonadal growth oscillates in a circadian manner and that the circadian rhythm of photosensitivity may be used by birds for photoperiodic time measurement. Some of these experiments suggest that circadian rhythms of motor activity and photosensitivity are phase-locked or tightly coupled (see, for example, in House Sparrows, Menaker, 1965; Menaker & Eskin, 1967; Farner et al., 1977). Therefore, various phases of the photosensitivity rhythm during its circadian cycle can be inferred from the pattern of motor activity and the photoinducible phase occurs during the latter portion of a cycle.

The effect of pinealectomy on the ontogeny or photoperiodically accelerated growth of reproductive organs of domesticated birds is equivocal (Menaker & Oksche, 1974). Pinealectomy has no effect on photoperiodically induced growth or maintenance of gonads in photoperiodic species under normal photoperiods or constant light (Menaker & Oksche, 1974; in House Sparrows, Menaker et al., 1970; Takahashi et al., 1978; in Starlings, Gwinner, 1977). Although these results suggest that the role of the pineal, if any, in photoperiodic gonadal growth in photoperiodic species is not an endocrine one (i.e., direct effects of its products on the hypothalamo-pituitary-gonad-axis), they do not exclude the possibility that the pineal plays a role in photoperiodic responses via its control of the circadian rhythm of photosensitivity. The results of experiments with normal photoperiods do not rule out this possibility, since pinealectomized birds remain entrainable to light-dark cycles. A critical test may require photoperiodic conditions that elicit the fairly subtle changes in the pattern of entrainment that are known to be produced by pinealectomy (Gaston, 1971; Takahashi et al., 1978). In order to test the hypothesis that the pineal has a role in photoperiodic time measurement I have conducted T-cycle experiments in pinealectomized House Sparrows and Starlings. T-cycles have been successfully employed by Farner et al. (1977) to explain the ultra-short-day response (gonadal growth to daily photoperiod shorter than 3 hours) in House Sparrows and by Elliott (1976) in Hamster photoperiodic testicular growth in accordance with the Bünning hypothesis. An ultra-short-day response has also been reported in Starlings (Schwab, 1971). The light-dark cycle of 26-h duration with a 3-h light pulse was used in the present studies.

Department of Zoology, University of Texas, Austin, Texas 78712, U.S.A.

Materials and methods

House Sparrow experiment

Adult male House Sparrows, *Passer domesticus,* captured on the grounds of the Max Planck Institute in Erling in the spring of 1977 were held in outdoor aviaries until 5 July, when they were transferred to an air-conditioned room (20 ± 2 °C) with 8 h of light per day (8L : 16D). The birds were housed individually in activity-recording cages and perch hopping was recorded on an Esterline-Angus event recorder. The birds were not acoustically or visually isolated from each other and the room was not equipped with a random noise generator. The average light intensity in cages was 200 lux. Food and water was available ad lib. After one month of 8L : 16D the photoperiod was changed to constant dark (DD). Two weeks thereafter pinealectomy or sham operation was performed in a manner similar to that described by GASTON & MENAKER (1968) under Nembutal anesthesia. Pinealectomy was judged as complete when the third ventricular choroid plexus was observed in the removed tissue under the dissecting microscope. The 3L : 23D regime was initiated one month after the surgery. Occasional laparotomies were performed to estimate testicular growth by measuring the width of the left testis. After the end of 3L : 23D cycles the birds were exposed to 12 days of constant light (LL) to ascertain if all birds were capable of growing testes. At the end of the experiment the birds were killed and left testes were weighed.

Starling experiment

Male Starlings, *Sturnus vulgaris,* caught near Mannheim, Germany, in the autumn of 1977 were held in outdoor aviaries until 5 December, when they were transferred to activity-recording cages in an air-conditioned room (20 ± 2, 8L : 16D). The average light intensity in the cages was 600 lux. Perch hopping was recorded on magnetic tapes and printed out in a graphical form similar to that provided by the event recorder. Pinealectomy was performed as in the Sparrows while the Starlings were held under 8L : 16D. On 22 December the 3L : 23D regime was initiated. On the same day a group of 6 birds were killed as initial controls. Another group of 6 birds were kept in a group cage in a light-tight box under 8L : 16D as intact short-day controls. Occasional laparotomies were performed to estimate testicular growth by measuring the width of the left testis. The experiment was terminated after 54 cycles.

In both experiments the phase angle difference in hours between the onset of activity and the onset of the light pulse was determined from the graphical records. The mean phase angle difference for the individual bird is a mean for the entire period beyond cycle 10. Statistical analyses were made with the Mann-Whitney U-test and Student's t-test.

Results

House Sparrow experiment

Sham pinealectomy had no appreciable effect on free-running activity. Pinealectomy induced large increases in activity time in all birds. Two out of eight pinealectomized (pinx) Sparrows became constantly active and another two nearly so. However, in all cases more or less discernible circadian periodicities remained and were invariably

shorter than preoperative periods and shorter than 24 hours. The behavior of the pinx Sparrows in this experiment were similar to those of pinx Starlings (GWINNER, 1978) and were different from those of pinx Sparrows in MENAKER's laboratory (GASTON & MENAKER, 1968; ZIMMERMAN & MENAKER, 1975). This difference may be due to differences in acoustical conditions used in respective experiments.

The effect of pinealectomy on testis growth under the 3L : 23D regime was markedly inhibitory (Fig. 1). The testes of the sham group grew and the mean width of left

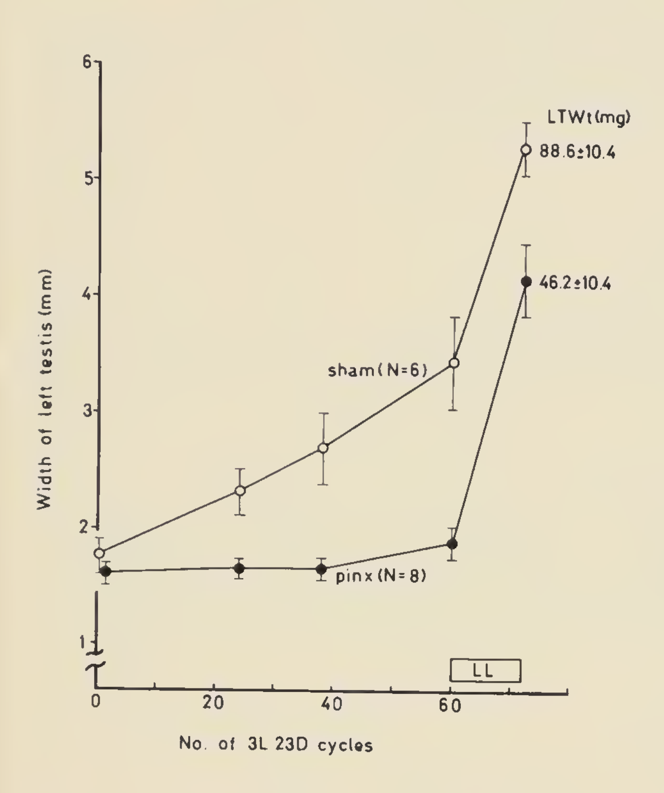


FIGURE 1. Effect of pinealectomy on photoperiodic testicular growth in House Sparrows exposed to the 3L : 23D regime. Testis growth of pinealectomized (pinx) and sham-operated (sham) Sparrows is expressed in width of left testis (mm). Sixty cycles of the 3L : 23D regime were followed by 12 days of constant light (LL). Vertical bars are standard errors. Figures on the right are means ± SEM of left testis weight (LTWt) at the end of the experiment.

testes was significantly greater than that of the pinx group throughout the entire period. Estimated mean weights of left testes of the sham and pinx groups after 60 cycles were 21 and 4 mg, respectively. During the 12 days of LL the testes of both groups grew. However, the mean left testis weight of the sham group was significantly greater than that of the pinx group, undoubtedly reflecting the difference in testis size at the beginning of the LL exposure. Both sham and pinx birds entrained to 3L : 23D cycles. The mean phase angle difference between the onset of activity and the onset of the light pulse for the sham group was 11.23 h (range 9.11—12.64 h) and for the pinx

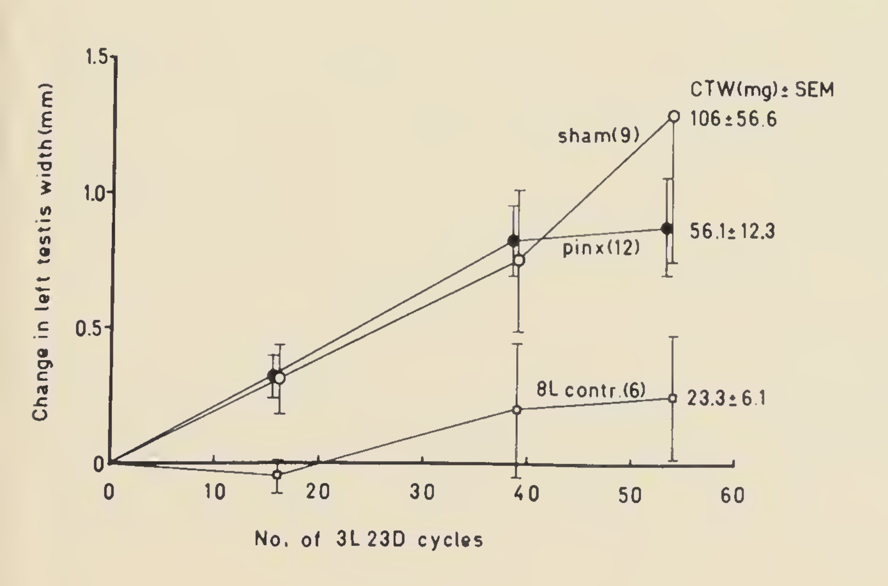


FIGURE 2. Effect of pinealectomy on photoperiodic testicular growth in European Starlings exposed to the 3L : 23D regime. Testis growth of pinealectomized (pinx), sham-operated (sham) and intact short-day control (8L contr.) Starlings is expressed as change in the width of left testis (mm) from day 0. Vertical bars are standard errors. Figures on the right are means ± SEM of terminal combined testis weights (CTW).

group was 12.54 h (11.45—14.08 h). Although this difference of 1 h 20 min is in the direction expected on the basis of GASTON's report (1971), it is not significant.

Starling experiment

There was a significant increase in testis width in both sham and pinx groups that was highly variable among individuals (Fig. 2). Actual mean widths ± SEM (mm) of left testes at the beginning and at the end of the experiment were: sham, 1.61 ± 0.08, 2.91 ± 0.57 (N = 9); pinx, 1.62 ± 0.07, 2.65 ± 0.21 (12); 8L control, 1.63 ± 0.14, 1.88 ± 0.24 (6). The sham and pinx Starlings entrained to 26-h cycles with mean phase angles of 13.51 h (range 10.33—15.89 h) and 14.53 h (12.68—17.02 h), respectively, the difference being non-significant.

Discussion

Growth of the testes of the sham-operated sparrows exposed to the 3L : 23D regime confirms the results of FARNER et al. (1977). The failure of the pinx sparrows to grow testes is one of the clearest demonstrations so far of the effect of pinealectomy on photoperiodic testicular response in birds. This observation is similar to that of TAKAHASHI et al. (1978) in pinx House Sparrows exposed to a stimulatory skeleton photoperiod of 13 hours with two one-h light pulses. Since the pinx sparrows were able to grow testes under LL, it is unlikely that they were photorefractory and it also appears unlikely that the observed effect of pinealectomy under 26-h cycles was of endocrine nature (i.e., a direct effect of the deprivation of pineal products on the hypothalamo-pituitary-gonad axis). Despite the significant difference in testis growth between the two groups there was only a minor difference in phase angles under entrainment to 26-h cycles. The difference in phase angles may not be solely responsible for the difference in testis growth. It is possible that the pinealectomy in some unknown manner affected the mechanism of photoperiodic time measurement. Whether the pineal is involved in the control of phases or coupling of oscillators controlling circadian rhythms of motor activity and photosensitivity remains to be elucidated.

It is by no means certain whether the effects of pinealectomy on photoperiodic testicular growth are the same regardless of the time of the year experiments are performed or the state of photosensitivity of birds. TAKAHASHI et al. (1978) obtained a significantly inhibitory effect of pinealectomy on testis growth of House Sparrows exposed to the skeleton photoperiod only in an experiment initiated in late January but not in experiments initiated in late December or early March. TUREK (in this volume) reported that pinx Sparrows exposed to 3L : 21D cycles in late winter tended to grow testes faster than the sham birds and tended to show greater phase advance. It, therefore, appears possible that the effect of pinealectomy on testis growth under certain prescribed photoperiods may depend on such factors as the time of the year, photosensitivity or other history dependent aspects of the bird's physiology.

The results of the Starling experiment indicate that the pattern of motor activity under entrainment to 26-h cycles are in agreement with the predictions based on ESKIN's model of entrainment (ESKIN, 1971). Twenty-six-hour cycles with 3 h light pulses stimulate testis growth in both sham and pinx Starlings despite much shorter duration of light available than the 8L : 16D regime is not stimulatory. The relatively

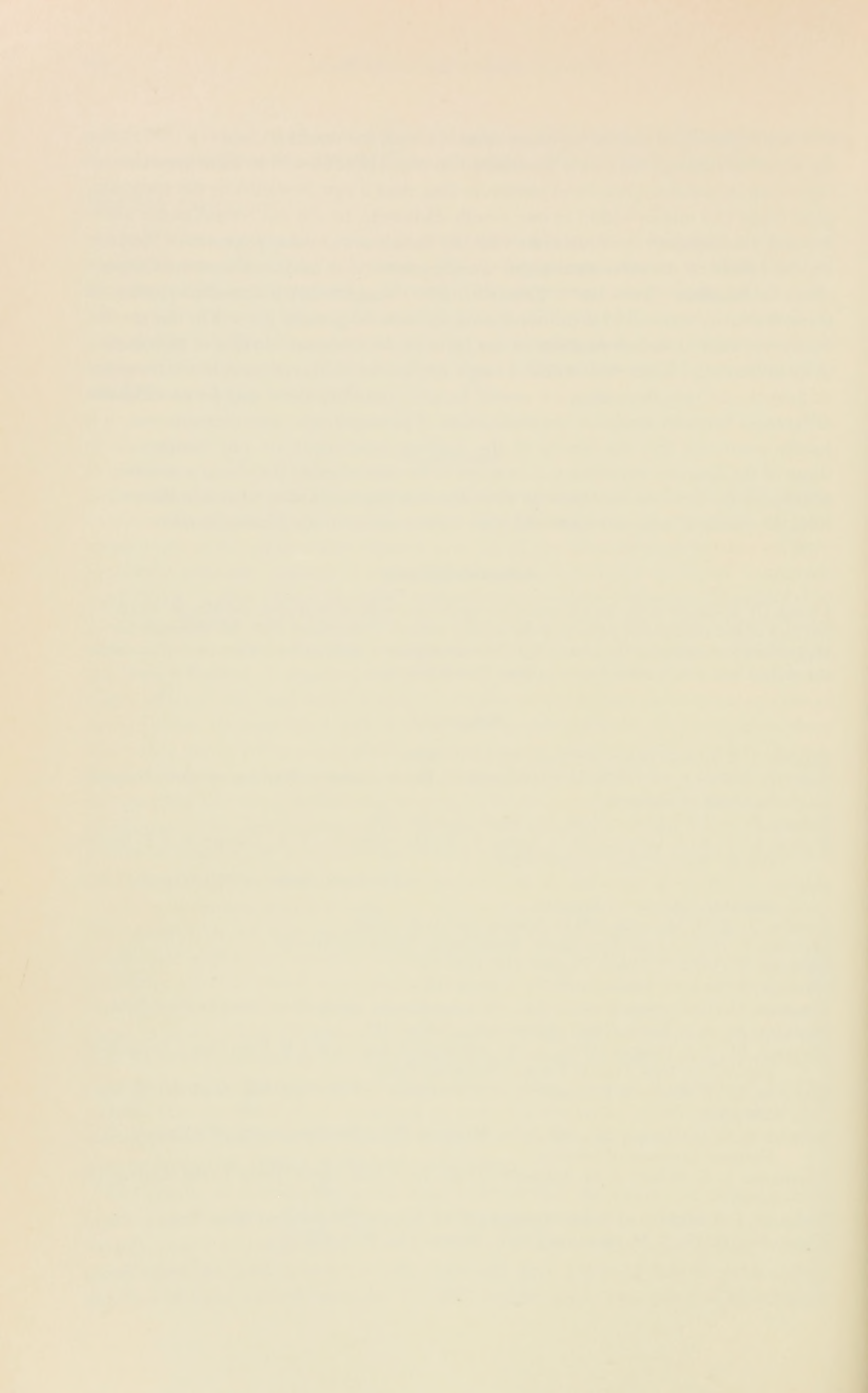
slow testis growth of the 26-h groups contrasts with the results of Schwab (1971) that the testes of starlings that were transferred to 3L : 21D (T = 24 h) after spontaneous regression in summer grew from minimum (less than 2 mm in width) to the spermatogenic stage (5.5 mm in width) in one month. However, he did not record motor activity, and, consequently, it is not clear whether the ultra-short-day response in Starlings may be caused by the same mechanism as in Sparrows. The results of resonance experiments in Starlings (Gwinner & Eriksson, 1977) suggest that a circadian rhythm of photosensitivity is involved in photoperiodically induced gonadal growth in this species. However, there is no information on the form of the circadian rhythm of photosensitivity in Starlings. Since even within a single species the effects of pinealectomy on testis growth can vary depending on several factors, and since there may be considerable differences between species in the mechanism of photoperiodic time measurement, it is hardly surprising that the results of the Starling experiment are not comparable to those of the Sparrow experiment. It remains to be seen whether the pineal is involved in photoperiodic time measurement at all in the Starling and under what conditions and how the pineal affects photoperiodic time measurement in the House Sparrow.

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SYMPOSIUM ON
CONTROL OF ANNUAL RHYTHMS

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Annual Endocrine Cycles in Male Teal *(Anas crecca)* and Peking Ducks *(Anas platyrhynchos)*

Monique Jallageas and Ivan Assenmacher

Introduction

Since Benoit's (1934) first description of the light-responsiveness of sexual function in domestic drakes, an impressive series of basic concepts in avian endocrinology, and more especially in the neuroendocrine control of reproductive cycles have evolved from experimental studies with domestic ducks. Of particular significance were the discovery of the central role of the anterior pituitary (Benoit 1935), of the hypophysial portal vessels and of the hypothalamus (Assenmacher & Benoit, 1953; Assenmacher, 1958), as well as the demonstration of the neuroendocrine role of the so-called extraretinal (diencephalic) photoreceptors (Benoit, 1938), that may bypass the otherwise direct retino-hypothalamic nervous route (Bons & Assenmacher, 1973); all findings related to the photogonadal response in ducks which led ultimately to far ranging generalizations.

More recently the experimental evidence from drakes, of marked hormonal interactions between testis, thyroid and adrenal has prompted to the assumption of closely interlinked endocrine cycles related to the reproductive cycle (Jallageas et al., 1974, 1978 b); Assenmacher et al., 1975, 1977).

In an attempt to explore whether the hormonal relationships that seem to prevail in domestic ducks may be extended to wild species of Anatidae a comparative study was initiated on two large flocks (around 100 specimens each) respectively, of male Peking ducks and of teal that were captured in the Camargue sanctuary in late fall. The two groups of birds were kept in outdoor parks, located on the University Campus of Montpellier (ducks) and in close vicinity to the seashore (teal) (Latitude 43° 50'N) (further details in Jallageas et al., 1978).

Annual endocrine cycles in male ducks

Reproductive cycle

In this experiment (Fig. 1) the annual variations in the plasma concentrations of LH and testosterone (Radioimmunoassays) occurred in close parallelism. Both hormones started to increase with increasing daylength, and reached maximal levels (4.3 ± 0.4 ng/ml for LH and 57.4 ± 5.9 ng/10 ml for testosterone) during the reproductive season that extended from March through May. Enlargement of the testis was delayed by one month, but culminated also in April-May (120 ± 9.0 g). The post-nuptial phase of the sexual cycle exhibited a peculiar pattern. Mating ceased almost suddenly in early June, when the LH and testosterone titers decreased toward minimal levels, that were already attained in July, but were followed in August by a transient rebound of both hormones: two fold LH and four fold testosterone respectively. Basal hormonal levels were finally attained in October (1.67 ± 0.34 ng/ml for LH, and 6.6 ± 1.8 ng/10 ml for

University of Montpellier II and ERA 85—CNRS, 34060—Montpellier (France)

testosterone). Along this time testis size displayed only a very transitory and reduced (50 %) regression in late June, and decreased then steadily from July to a minimum in November (2.2 ± 0.3 g).

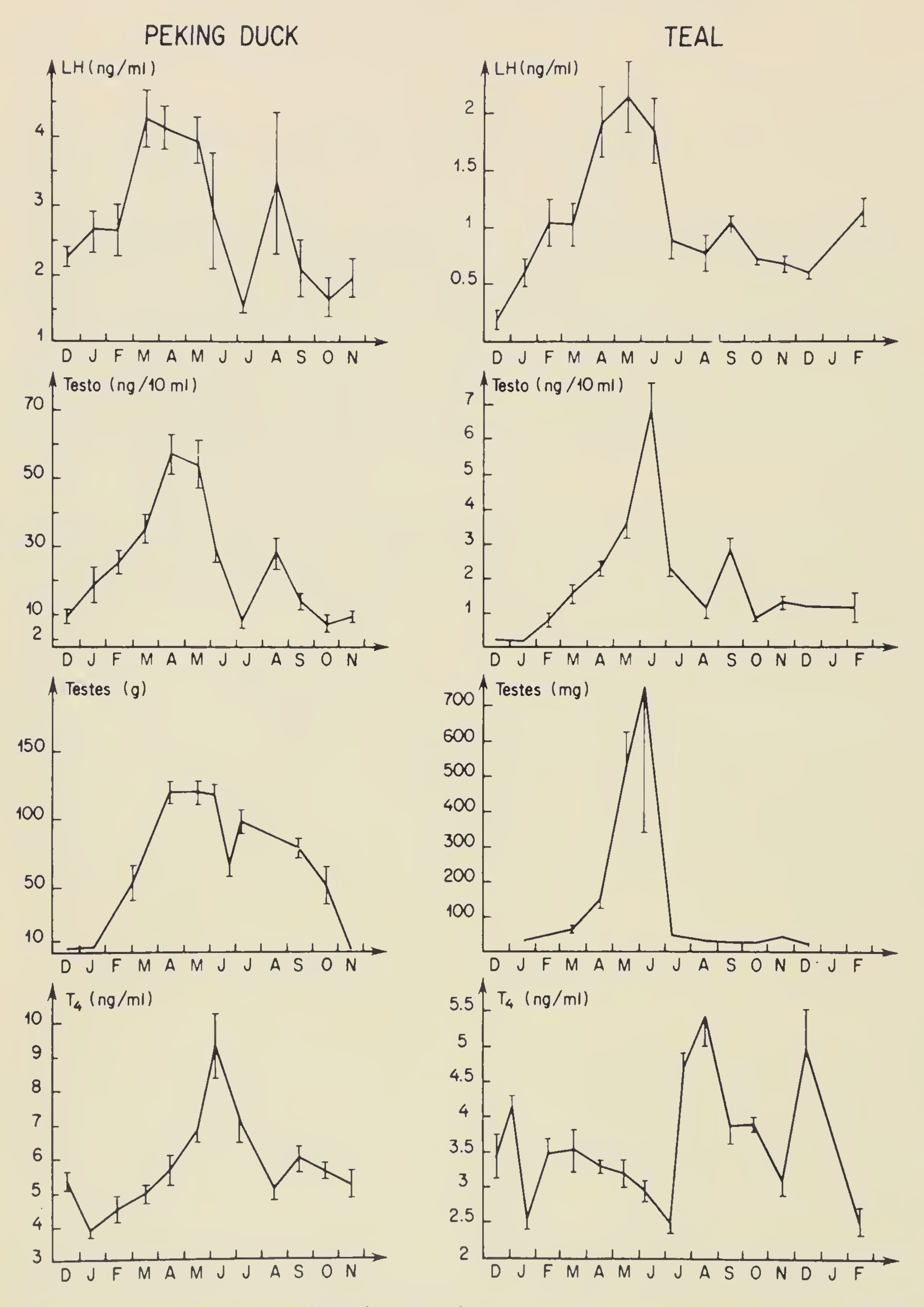


FIGURE 1. Annual endocrine cycles in Peking ducks and teal. Standard errors below 2 g (ducks) or 10 mg (teal) for testis weights, and below 0.1 ng for testosterone were not indicated on the graphs.

The polyphasic profile of the testosterone cycle appears as a very constant feature in domestic ducks whether Peking (GARNIER, 1971; JALLAGEAS et al., 1974) or Rouen (BALTHAZART & HENDRICK, 1976). Although the metabolic clearance rate (MCR) of the

androgen has been shown to be augmented by about 70 % in June, the estimated secretion rate (SR) of the hormone nevertheless decreased significantly through the summer trough (June-July) in plasma testosterone (Assenmacher et al., 1975). On the other hand the LH concentrations, which paralleled closely in this experiment the testosterone titers, may stay at least in some specimens at elevated levels through June and July (Jallageas et al., 1974; Haase et al., 1975 a). Regarding testis weight, the critical period in June-July never was associated with a marked regression involving a blockade of spermatogenesis.

Thyroid cycle and molt

Whether appraised by the plasma concentrations in thyroxin (Fig. 1), or by functional estimations using labelled iodine (Astier et al., 1970) the thyroid function of the Peking duck displayed an annual cycle with a two-fold (Fig. 1) to three-fold (Assenmacher et al., 1975) increase of plasma thyroxine titers in June. It should be stressed that the annual peak in thyroxine levels was always found to coincide with the post-nuptial molt, that extended in this experiment from mid June to mid July. Previous studies have shown that experimentally induced (ectopic pituitary transplantation) molts could be prevented either by testosterone replacement therapy (Assenmacher & Baylé, 1968) or by pharmacological blockade of thyroxine synthesis (Baylé, 1972); it is assumed that the annual post-nuptial molt actually resulted from the seasonal imbalance of the thyroxine/ testosterone ratio, that underwent a steep increase in June-July.

Testis-thyroid interactions

From a series of experiments on the effects of varying testosterone titers on the thyroid function (Jallageas & Assenmacher, 1972) and of varying thyroxine levels on the male sexual function (Jallageas & Assenmacher, 1974; Jallageas et al., 1974) it was concluded that increased concentrations of either hormone depressed the opposite endocrine function. It was shown in particular that administration of physiological doses of thyroxin in sexually active ducks (April) could be compatible with maintained high LH levels, but always induced a decrease in plasma testosterone (Jallageas et al., 1974), together with a complete regression of the cell organelles in the endocrine testis (Jallageas et al., 1978 a), thus leading to a state which is reminiscent of the natural situation in June. This strong evidence of a reciprocal inhibitory interaction between the endocrine testis and thyroid raised therefore the question of a possible interference between both endocrine functions during the critical postnuptial phase of the annual cycle (June through September) when the testosterone and thyroxine cycles are progressing in phase opposition.

This assumption was further strengthened by the effect of either thyroidectomy or castration on the annual endocrine cycles (Jallageas et al., 1978 b; Assenmacher & Jallageas, 1978).

Thyroidectomy (March) led to a two to three-fold increase vs intact controls in LH from June to September, followed by a downfall in October. The biphasic pattern of the cycle had disappeared. Concomitantly the testosterone levels were also augmented by about three times, although a slight depression was still apparent in June. The transient decrease of plasma LH and testosterone in June, which leads to the peculiar

bimodal profile of both hormones during the postnuptial phase of intact ducks appears therefore principally due to the annual peak in thyroxine secretion. In contrast, the autumnal depression of the gonadotropic system appears unrelated to thyroid-testis interactions, and could rather result from the decreasing daylength.

Gonadectomy (November) on the other hand altered the thyroid cycle by raising plasma thyroxine from January through August to the annual peak levels, thus indicating that in intact birds the increasing testosterone secretion in spring actually inhibits the thyroid function until late May. On the other hand, the autumnal decline in plasma thyroxin again appeared unrelated to testis-thyroid interactions.

Annual endocrine cycles in male Teal

Reproductive cycle

Although the progressive phase of the sexual cycle appeared in teal slightly delayed as compared with the neighbouring flock of Peking ducks (Fig. 1) it also coincided with increasing daylength, thus confirming teal as long day breeders.

Sexual behaviour including call and nuptial display (the flock comprised fourty female birds that were not otherwise studied) increased progressively from February to June, in close relationship with augmenting testosterone and LH levels, and with testicular weights. Plasma LH was elevated by three times above winter levels from April through June, whereas the testosterone concentrations appeared steadily increasing until June, when they exceded by about 30 times the titers measured in January. Although testis enlargement paralleled fairly well the raising hormone titers, the increasing standard errors (Fig. 1) of the testicular weights from April to the climax in June (743.3 ± 416.6 mg) attested that only a few birds attained fully developed testes weighing above 2.000 mg (the maximum was 4,174.7 mg). Subsidarily it should be stressed that in the female birds neither nesting nor egg laying was observed. The difficulty encountered by captive teal to reach maximal testicular enlargement was also reported by CHAN (1971) and LOFTS (1975) who were unable to observe spermatogenetic testes in teal kept captive over one year in Hong Kong (Lat. 22° N) unless they were provided artificial "long days" (17 L-7 D) from April onward. In a recent study with bioclimatic chambers provided with artificial photoperiods (18 L-6 D) in January, a group of 10 teal attained within 4 weeks a maximal testis weight (933.6 ± 234.0 mg) that was very close to the June values of their outdoor living congeners (JALLAGEAS et al., 1978 b).

The postnuptial phase of the sexual cycle in teal revealed a conspicuous analogy with Peking ducks regarding the hormonal parameters. As a matter of fact the plasma levels in LH and testosterone fell down by July through August to near basal values, and underwent then a transient rebound in September, before reaching the autumnal minimum. Correlatively, the birds were lacking any sexual behaviour from mid-June through August, but they resumed in September isolated components of song and sexual displays. A very similar biphasic cycle in plasma LH has also been reported for wild mallard ducks studied in Kiel (Lat. 54° N) by HAASE et al., (1975 b), and may therefore reflect a rather common pattern among Anatidae whether domestic or wild.

However unlike in Peking ducks, the testes in teal underwent a complete regression in early July without any recrudescence in late summer. Whether or not this peculiar aspect of the testicular cycle in teal may be ascribed to captivity is unknown.

Thyroid cycle and molt

As estimated by the plasma concentrations in thyroxine, the thyroid cycle of teal appeared more complex than in Peking ducks. In good agreement with the Peking duck cycle, the plasma thyroxine levels in teal exhibited a seasonal, twofold peak in July-August, in close correlation with the postnuptial trough in plasma LH and testosterone.

This could indeed result from reciprocal testis-thyroid interactions similar to those that were discussed for the same phase in Peking ducks. On the other hand teal as well as Peking ducks underwent the postnuptial molt leading to the eclipse plumage during this particular phase of thyroxine/testosterone imbalance.

However unlike ducks, the teal displayed a second seasonal peak in plasma thyroxin in early winter. Although this renewed increase in thyroid function appeared related with prenuptial molting, which occurred in fact later in the captive teal than in wild specimens (TAMISIER, 1972), it could also result at least partially from the low ambient temperature, since December and January were the coldest months of the year.

Conclusion

The comparison of the sexual and thyroid cycles in outdoor-living Peking ducks and teal have revealed striking analogies together with a few discrepancies. (1) Both species started their annual sexual cycle, as appraised by plasma LH and testosterone concentrations and by testis weight, in close correlation with increasing daylength. The climax of the cycle occurred, respectively, in April-May (ducks) or May-June (teal). Complementary studies in bioclimatic chambers could demonstrate the light sensitiveness of the sexual function for both species. However, only a restricted number of captive teal, whether living outdoors or indoors attained maximal testicular enlargement. (2) The postnuptial phase of the sexual cycle was also characterized in both species by a biphasic pattern of plasma LH and testosterone, which fell down in early June (ducks), or July (teal), and rebounded two months later, before reaching finally basal levels in autumn. In ducks the hormonal downfall in June was associated with a moderate and transitory regression in testis size, which attained full regression only later in autumn, whereas in teal testicular regression was already achieved in July. (3) Sexual behaviour in teal paralleled the testosterone cycle. (4) In both species, plasma thyroxine levels attained a maximum at the very beginning of the postnuptial phase. The annual maximum in thyroid function, associated with the steep depression in testosterone secretion, coincided with the postnuptial molt. An additional increase in plasma thyroxin appeared in teal in early winter and was then correlated with both the prenuptial molt and with the lowest ambient temperatures measured throughout the experiment. (5) A series of experimental observations in ducks, including studies of the endocrine cycles in thyroidectomized or gonadectomized birds have led to the assumption of close interactions between the sexual and the thyroid cycles. As a matter of fact the vernal increase in testosterone secretion appears to induce thyroid inhibition, whereas the in-

creased thyroxine secretion in June may be responsible for the strong inhibition of testosterone secretion during the early postnuptial phase.

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The Control of the Annual Gonadal Cycle of Wild Mallard Drakes: Some Endocrinological Aspects

Eberhard Haase

Introduction

The endocrine events during the annual reproductive cycle of birds and the physiological basis of photo-sensitivity and photorefractoriness are only partially known. Nevertheless, there are numerous hypotheses with respect to these subjects which are mostly based on circumstantial evidence. Due to the recent development of new techniques for the direct measurement of hormones, one can describe the reproductive cycle and the states of photosensitivity and photorefractoriness more closely. Using experimental approaches we wanted to find out whether hormonal antagonisms of feed-back mechanisms contribute to the control of the annual periodicty of reproduction.

The annual cycle of Mallard drakes

Testicular weight

Our drakes were kept in large outdoor aviaries in Kiel (54° N), Germany. The seasonal weight changes of their testes were equal to those of free living specimens (Paulke, 1975). During the greatest part of the year the testes were small (< 1 g). An obvious weight increase was observed in February, maximal weights (20—25 g) were found in April and May. Testicular regression started by the end of May / early June and in a few weeks minimal weights were reached.

Luteinizing hormone

For the determination of LH and the gonadal and thyroidal hormones of intact birds, blood samples were taken from 9 individually marked drakes at the beginning of each month over a 2 years period.

The LH concentrations were high during the reproductive phase in both years (Haase et al., 1975 and unpubl.). At the time of the testicular involution there was a steep decrease of the LH levels (Fig. 1). Thus, the onset of photorefractoriness seems to be characterized by decreasing LH concentrations in the plasma of Mallards and other species (Follett et al., 1975; Nicholls, 1974; Sharp et al., 1975). With respect to this gonadotropin the antigonadal effect of prolactin (Meier, 1969; Meier & Mac Gregor III, 1972) contributes little to the understanding of photorefractoriness.

As in the Herring Gull (Scanes et al., 1974) and the Red Grouse (Sharp et al., 1975) an autumnal increase of the plasma LH levels was found in the Mallard. It occurred under rather short and decreasing photoperiods. A circadian basis of the photoperiodically induced LH secretion as it has been described for the White-crowned Sparrow

Co-author: Edgar Paulke

Author's address: Institut für Haustierkunde, Christian-Albrechts-Universität, 2300 Kiel, Bundesrepublik Deutschland

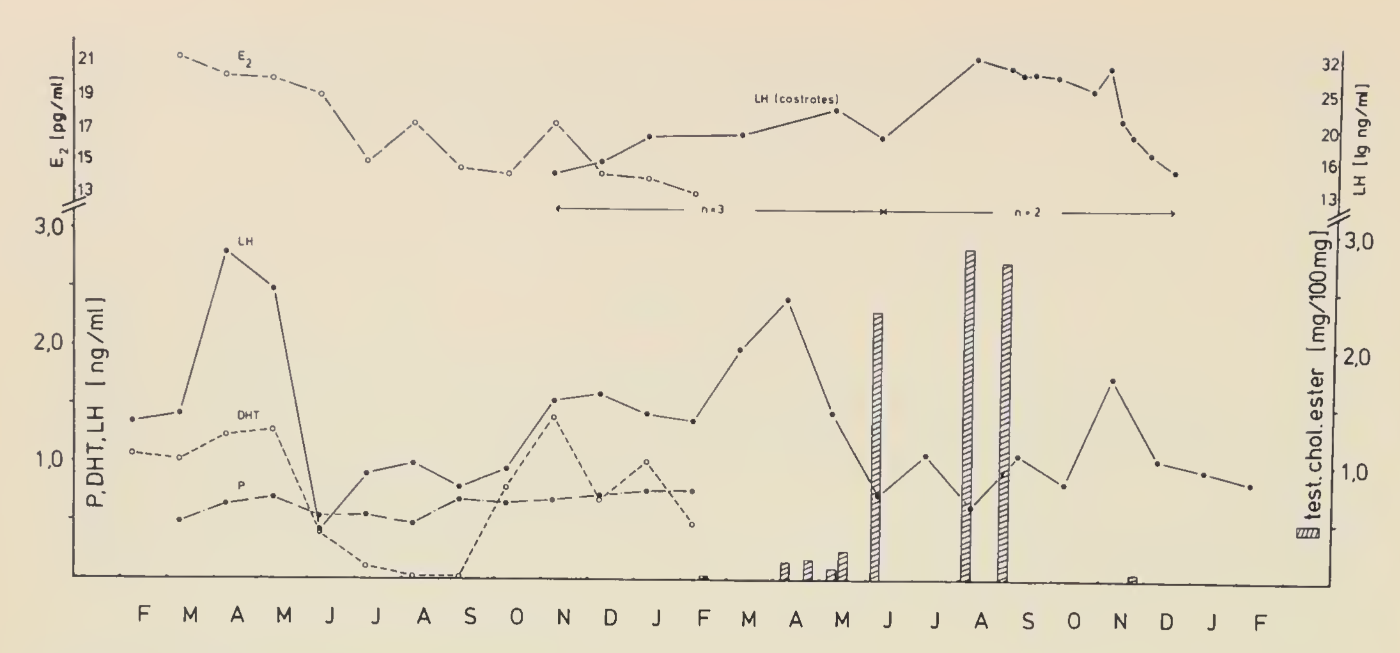


FIGURE 1. For explanation see the text.

(FOLLETT et al., 1974) may nevertheless hold for the Mallard if phase shifts are assumed (see FARNER et al., 1977).

Androgens

In both years the seasonal fluctuations of the plasma testosterone levels were very similar to those of LH and there was a significant linear correlation between the monthly means of the 2 hormones (Fig. 1, 2) (PAULKE & HAASE, 1978). A disassociation between testicular size, LH and testosterone at the end of the breeding season as it has been described for Peking drakes (JALLAGEAS et al., 1974) did not occur in our wild Mallards.

The autumnal testosterone peak was probably caused by the elevated LH levels and was not accompanied by a testicular weight increase. Its biological meaning seems to be the elicitation of display and sexual behavior (ETIENNE & FISCHER, 1964) which can be frequently observed during this time of the year (RAITASUO, 1964).

The seasonal pattern of the DHT concentrations was similar to those of LH and testosterone (Fig. 1) and the monthly means were linearly correlated (PAULKE & HAASE, 1978). The DHT: testosterone ratio seems to be rather high in birds (WINGFIELD & FARNER, 1975; FEDER et al., 1977). Perhaps plasma DHT plays an important role as

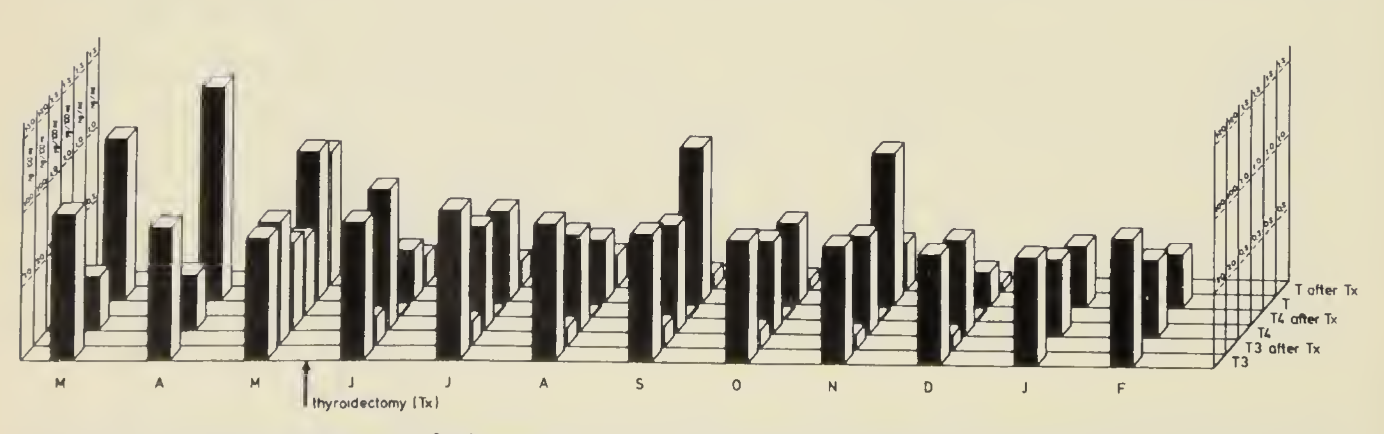


FIGURE 2. Seasonal changes of plasma T3, T4 and T levels in intact thyroidectomized wild Mallard drakes.

active feed-back inhibitor in the gonadotropic hypothalamo-hypophyseal system of birds (PAULKE & HAASE, 1978).

Cholesterolesters, Estradiol, Progesterone

In the testes of many bird species Schultz-positive lipids accumulate during testicular regression and are abundant during the refractory period (LOFTS, 1970; HAASE, 1973). As posible precursors of steroid hormones they might be important links in the control of the gonadal cycle (LOFTS, 1970). A quantitative biochemical analysis of different lipid fractions of Mallard testes showed that the concentrations of cholesterol and especially cholesterolesters were high during the refractory period (HÖFFER, 1975) (Fig. 1). It is, however, not yet clear whether this resulted in significant changes of total cholesterolesters of the testes.

There were no significant seasonal changes in the plasma progesterone concentrations of our wild Mallard drakes (Fig. 1) (PAULKE, 1975). Thus, the increase of the testicular concentrations of cholesterol and cholesterolesters at the beginning of the refractory period did not lead to an elevated progesterone secretion in Mallards.

Since the peak in August was not significantly different from the values found in July and September the concentrations of estradiol-17 β were high mainly during periods with elevated androgen levels (Fig. 1, 2) (PAULKE, 1975). An increased estradiol secretion during the refractory period (LOFTS, 1970) is not supported by these findings. The higher estradiol levels during the reproductive season probably induce the post-nuptial eclipse plumage. This is in agreement with the results of castration experiments of WALTON (1937) and CARIDROIT (1938).

Thyroidal hormones

In most bird species reproduction and molt do not overlap and there seems to be a certain hormonal antagonism between these two events (ASSENMACHER, 1958; PAYNE, 1972). JALLAGEAS & ASSENMACHER (1974) discuss the increased plasma thyroxine concentration at the onset of molt as a possible cause for testicular regression.

The concentrations of T3 and T4 in the plasma of our drakes showed maximal values at the begin of the refractory period in June (T3) and July (T4) (Fig. 2) (HAASE & PAULKE, in prep.). During this time of the year, the highest thyroxine and $PB^{131}I$ levels have also been found in Peking drakes (ASSENMACHER et al., 1975). Consequently, at the end of the reproductive season there is an opposite trend in the concentrations of reproductive and thyroidal hormones. Thyroidectomy should help to solve the problem of a possible mutual suppression.

Experimental interferences

Thyroidectomy

Thyroidectomy in birds has resulted in conflicting data with respect to reproductive parameters. Whereas WIESELTHIER & VAN TIENHOVEN (1972) could demonstrate a stimulating effect on testicular size and androgen secretion in the Common Starling, *Sturnus vulgaris,* THAPLIYAL & CHATURVEDI (1976) reported a decrease in testes weight in the Indian Mynah, *Acridotheres tristis,* another starling. In domestic drakes testicular

growth and spermatogenesis were stimulated by the presence and inhibited by the absence of thyroidal hormones (see BENOIT, 1937).

Radiochemical thyroidectomy of 8 wild Mallard drakes at the end of the reproductive season severely disturbed the post-nuptual molt. The plasma levels of T3 and T4 steeply decreased and did not recover until the end of the experiment. Plasma testosterone concentrations also dropped and remained significantly lower than in intact birds, though a slight autumnal peak could be observed (Fig. 2). Seven drakes which died during the winter had small testes. In the only surviving bird the plasma testosterone level did not increase during the next spring and there were no signs of spermatogenesis. Therefore, the absence of spermatogenesis during summer, autumn and winter in the annual cycle of wild Mallard drakes cannot be overcome by thyroidectomy. Our thyroidectomy results do not favor the idea of a mutual suppression of reproductive and thyroidal hormones as an important factor in the control of photorefractoriness.

Castration

Castration can contribute to elucidate the role of the negative feed-back between gonads and hypothalamo-hypophyseal system in the control of the reproductive periodicity. In several bird species (STETSON & ERICKSON, 1971; MATTOCKS et al., 1976; WILSON & FOLLETT, 1974; NICHOLLS & STOREY, 1976; HAASE, unpubl.) castration did not significantly alter the duration of the gonadotropic activity of the pituitary and the onset of the refractory period. Findings in uni- and bilaterally castrated domestic drakes also oppose the participation of the testes in photorefractoriness and favor the pituitary or the nervous system as the site of photorefractoriness (BENOIT et al., 1950). During the course of the reproductive season the hypothalamo-hypophyseal system of domestic drakes becomes increasingly sensitive to exogenous testosterone (KORDON & GOGAN, 1970).

We have castrated 3 wild Mallard drakes in August and determined LH in blood samples from different seasons (Fig. 1). In the autumn the LH levels reached about ten fold of the normal values. They remained high during winter, spring and summer and seemed not to depend on the natural fluctuations of the photoperiod. During the summer there were no signs of a photorefractoriness of the LH secreting system which points towards the participation of the testes in the control of the cycle. These preliminary findings contradict those in passerine species (see above), and perhaps different systematic groups use different physiological mechanisms for the control of their reproductive cycles. Nevertheless, a negative feed-back via steroid hormones cannot be excluded in songbirds unless the role of the adrenals is known. Our results are not necessarily at variance with those of BENOIT et al. (1950) who castrated their drakes shortly before testicular regression. It might be that at this time the negative feed-back had already induced photorefractoriness.

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Circadian Components of the Circannual Mechanism in the White-throated Sparrow

Albert H. Meier, Blaine R. Ferrell and Larry J. Miller

Introduction

The White-throated Sparrow, *Zonotrichia albicollis,* is a passerine migrant of eastern North America. Because its life history and annual cycle are well known (Eyster, 1954; Weise, 1956; Wolfson, 1958; Shank, 1959; Meier et al., 1969), this bird is ideal for investigations of physiological mechanisms. As in many other avian species of the temperate zone, the annual cycle is influenced by daylength. Increasing daylengths in spring initiate development of the reproductive system and vernal migration. However, after the young are raised, the adults become photorefractory and the reproductive system regresses in the summer when daylengths are still long.

Although daylength is an important synchronizer of the annual cycle, it is now clear that the principal timing mechanism in many birds (reviews, Gwinner, 1973, 1975, 1977; Berthold, 1974), including the White-throated Sparrow (Meier & Fivizzani, 1975), is an endogenous circannual mechanism. In birds kept indoors on constant daylengths, molt, gonadal recrudescense and regression, fattening, and migratory restlessness occur in a sequence which approximates that found under natural conditions. White-throated Sparrows maintained on 16 hour daily photoperiods beginning during the winter change progressively during the ensueing 10 months from winter to spring (gonadal recrudescense, increased body weight and fat stores, nocturnal migratory restlessness), summer (gonadal regression, decreased body weight and fat stores, absence of nocturnal activity, and molt) and autumn (increased body weight and fat stores and nocturnal migratory restlessness) conditions.

Photostimulation of reproductive indices in photosensitive birds has been shown to involve circadian rhythms (Hamner, 1963, 1964; Farner, 1964, 1965; Wolfson, 1965). It is thought that a circadian rhythm of photosensitivity is entrained by the daily photoperiod. If light coincides with a photosensitive phase it induces gonadotropin production, perhaps by coupling a second circadian oscillation that interacts with the photosensitivity rhythm (review, Meier & Ferrell, 1978).

Hormonal components of the circannual clock

Evidences of circadian components of the neuroendocrine system that might regulate a circannual cycle were first observed in the White-throated Sparrow. Prolactin injections during the afternoon (LD 16:8) in both refractory and photosensitive sparrows stimulated fattening and nocturnal restlessness characteristic of the migratory period whereas injections given early in the day were ineffective or inhibitory (Meier & Davis, 1967; Meier, 1969). It was further demonstrated that pituitary prolactin is released during the afternoon in sparrows tested during the vernal migratory period and near dawn in photorefractory birds in summer (Meier et al., 1969). Because day-

Department of Zoology and Physiology, Louisiana State University, Baton Rouge, LA 70803, U.S.A.

length is equivalent at the two seasons tested, the prolactin phase shift may be an expression of a circannual mechanism.

Photoperiodic entrainment of the circadian rhythms of metabolic and behavioral responses to prolactin apparently is mediated by a neuroendocrine mechanism that includes a circadian rhythm of corticosteroid activity. Corticosterone injections induced daily rhythms of responses to prolactin in White-throated Sparrows maintained in LL to remove photoperiodic cues. Daily injections of prolactin given 12 hours after corticosterone injections induced many conditions associated with the vernal migratory period, including gonadal growth, fattening, nocturnal migratory activity, and northward orientation in birds tested under the open night sky. Similarly prolactin injections at 8 hours after corticosterone injections (8-hour relation) elicited summer conditions (gonadal inhibition, loss of body fat, and suppression of nocturnal activity) and a 4-hour relation promoted autumnal conditions (fattening and nocturnal migratory activity oriented southward) (MEIER & MARTIN, 1971, MEIER et al., 1971, MARTIN & MEIER, 1974; MEIER, 1976).

Assays of plasma corticosterone in White-throated Sparrows further support corticosterone involvement in setting circadian rhythms of responses to prolactin. During the vernal migratory period, the daily rise of plasma corticosterone concentration occurs near dawn (DUSSEAU & MEIER, 1971; MEIER & FIVIZZANI, 1975). Thus there is a 12-hour interval between the daily rise of plasma corticosterone and the release of pituitary prolactin in birds in spring condition (MEIER et al., 1969). Early during the summer photorefractory period, the rise of plasma corticosterone occurs early during the dark (DUSSEAU & MEIER, 1971) so that there is a 6- to 8-hour relation between the corticosterone increase and the release of pituitary prolactin. After several weeks the corticosterone rhythm dampens out completely but reappears as a new distinct rhythm during the autumn migratory period (MEIER & FIVIZZANI, 1975). Seasonal changes in the plasma corticosterone rhythm occur in sparrows maintained in outdoor aviaries (DUSSEAU & MEIER, 1971) as well as indoors on constant 16-hour daily photoperiods (MEIER & FIVIZZANI, 1975).

The manner in which corticosterone and prolactin injections induce seasonal conditions in the White-throated Sparrow has not been fully established. However, it seems probable that gonadal development, nocturnal restlessness, and the orientational effects are consequences of hormone action on the nervous system. Timed daily injections of corticosterone and prolactin apparently organize entire neuroendocrine complexes appropriate for each season.

Inspired by observation in a fish that corticosteroid injections entrain circadian rhythms of fattening responses to prolactin which persist for at least 5 days after corticosteroid injections are terminated (MEIER, et al., 1969; 1971), we reasoned that daily injections of corticosterone and prolactin might also establish persistent circadian rhythms in the White-throated Sparrow. We further hypothesized that the temporal relation of two circadian neuroendocrine oscillations entrained by corticosterone and prolactin injections may be the basis of the circannual mechanism. This possibility has recently been tested in the White-throated Sparrow (FERRELL & MEIER, unpublished).

Two groups of sparrows were placed in LL and injected with corticosterone and prolactin in a 12-hour relation for 11 days. Birds in group 1 were finishing the post-

nuptial molt in late summer (August) and birds in group 2 were entering the autumnal migratory condition (increased fat stores and nocturnal migratory activity) in September. Most of the sparrows in each group responded to the injections by exhibiting vernal conditions and these birds were observed during the subsequent months when they remained untreated on 14-hour daily photoperiods. The results of group 1 are illustrated in Figure 1. The vernal conditions (gonadal stimulation, heavy fat stores, and

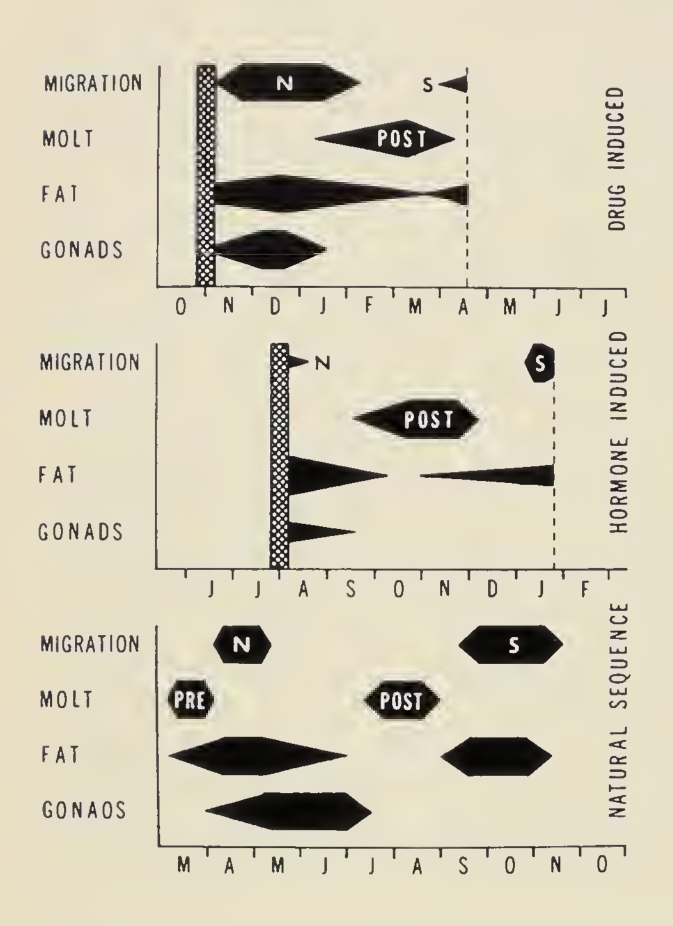


FIGURE 1. Hormone and drug induced alteration of the circannual cycle of the White-throated Sparrow, *Zonotrichia albicollis.* Injection period is indicated by cross-hatching and orientation of nocturnal activity is designated as N (northward) or S (southward). Treatment regimen and indices of the parameters measured are provided in the text.

migratory activity oriented northward) terminated 3 to 4 weeks, following hormone treatment. Postnuptial molt occurred subsequently in each group and was followed by fattening and nocturnal activity oriented southward. Although some of the birds did not exhibit the entire range of conditions noted, at least several birds in each group performed in a manner which suggests that the hormone injections set the phase of the circannual clock so that hormone-treated birds progressed from late vernal conditions in late summer to summer conditions in the autumn and to autumn conditions in the winter.

Neurotransmitter components of the circannual clock

It seemed likely that the resetting activities of corticosterone and prolactin injections might occur by way of known feedback influences of the hormones on their own production. The mammalian literature indicates that prolactin production is under inhibitory control by neurons that release dopamine (SHAAR & CLEMENS, 1974; HOROWSKI & GRAF, 1976). Prolactin in turn inhibits its own production by stimulating enzymatic activity that leads to the formation of dopamine and norepinephrine (MUDELSKY et al., 1977). Both catecholamines are important neurotransmitters of the brain and have many basic roles in neural activities in addition to the control of prolactin production.

Neural regulation of corticosteroid production at least with respect to its circadian rhythm, is not so well delineated. There are evidences for both stimulation and inhibition of corticosteroid production by serotonergic neurons, and corticosteroid may have both stimulatory and inhibitory effects on serotonin synthesis and activity. The most immediate effects of corticosteroid, however, appear to be stimulation of serotonin synthesis (Naumenko, 1968). Serotonin is also one of the most important neurotransmitters of the brain. Any effect on its production or activity may be expected to have profound influences on neural and hormonal events.

We reasoned that if corticosterone and prolactin resetting of the circannual clock is effected by way of influences on neurotransmitters then it should be possible to set the clock with drugs that simulate the hormonal activities. Accordingly 5-hydroxytryptophan (5-HTP, the immediate precursor of serotonin) could be substituted for corticosterone and dihydroxyphenylalanine (DOPA, a precursor for both dopamine and norepinephrine) could be substituted for prolactin. Thus in late October a group (7 birds) of birds in autumn condition were taken from an outdoor aviary and placed indoors in LL. Each bird was injected (s.c.) daily with 5-HTP followed in 11 hours by DOPA injections (s.c.). As added insurance that the timing of serotonin stimulation (with 5-HTP injections) would be precise, parachlorophenylalanine (PCPA, a potent long-lasting inhibitor of 5-HTP synthesis) was injected (s.c.) daily 4 hours after DOPA injections. A group of 4 uninjected birds were subjected to similar photoperiod treatment for comparative purposes.

After 2 weeks of daily injections, the birds were transferred to a photoperiodic regimen (LD 16: 8) in which they were retained for observation during the ensueing months. Compared with observations made before the injection period, significant gonadal growth (determined by laparotomy) was apparent in 5 of the 7 experimental birds. No gonadal change occurred in the 4 uninjected birds. Of the 5 responding birds, the testes (3 birds) and ovaries (2 birds) continued development until mid-December (see Figure 1). Fat levels also increased steadily following injections and paralleled gonad growth. The birds were active nocturnally during November and December and this activity was oriented northward in birds tested under the open sky. The onset of a complete molt of body and flight feathers in January coincided with a decline in both fat stores and gonad size. In April the fat levels increased and nocturnal activity reappeared. However, this time the activity was directed southward. These findings indicate that precursors for serotonin and catecholamine neurotransmitters injected daily in a specific temporal relation can reset the circannual mechanism of birds in autumn so that they enter an early stage of vernal conditions. This resetting by an 11-hour relation of 5-HTP and DOPA injections differs somewhat from that produced by a 12-hour relation of corticosterone and prolactin which reset the circannual mechanism in a late stage of vernal conditions.

Conclusions

A salient feature that emerges from these studies is that changing temporal relations between two circadian neural oscillations can account for the circannual changes in reproduction, metabolism, and behavior of the White-throated Sparrow. The circadian rhythms of corticosterone and prolactin are expressions of these oscillations; and injec-

tions of these hormones apparently set the phase of the neural oscillations by way of feedback influences on serotonergic and catecholaminergic neurons. Each neural oscillation may be composed of many parts that can be uncoupled. Both oscillations are probably responsible for the regulation of circadian neural and endocrine events in addition to the corticosterone and prolactin rhythms. Interaction of the two neural oscillations and their products may account for additional effects such as production of gonadotropic hormones. The changing relations of the neural oscillations are probably driven by the products of every preceeding temporal relationship. Much needs to be done to test this working hypothesis in the White-throated Sparrow and in other species. The theoretical and practical implications of our results mandate a major effort to understand the mechanisms involved.

Acknowledgements

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Temporal Aspects of the Secretion of Luteinizing Hormone and Androgen in the White-crowned Sparrow, *Zonotrichia leucophrys*

John C. Wingfield and Donald S. Farner

Introduction

The White-crowned Sparrow, *Zonotrichia leucophrys*, is a particularly useful species for investigations of the environmental and endocrine control of annual rhythms. Within this one species there are five races that show a wide spectrum of annual cycles ranging from a non-migratory race of coastal California to a migratory race that breeds over a vast area across Alaska and northern Canada and winters in southwestern U.S.A. (Cortopassi & Mewaldt, 1965).

As the literature on the reproductive biology of this species is now voluminous, discussion in this brief communication will be restricted to temporal changes in plasma luteinizing hormone (LH), testosterone and 17β-hydroxy-5α-androstan-3-one (DHT) in males, the relationships of these changes to the reproductive cycle and modifications thereof that can be induced by the environment.

Photoperiodic control

The role of the late winter and vernal increase in day length in the initiation and regulation of gonadal growth in this species is well documented (e.g. Farner, 1966; Farner & Lewis, 1971; Farner, 1975) and is currently thought to act primarily as a "driver" for the gonadal cycle rather than as a Zeitgeber for an endogenous circannual function (King & Farner, 1974; Farner, 1976; Farner & Follett, 1978).

The demonstration of endogenous circannual rhythms in *Phylloscopus* and *Sylvia* (Berthold et al., 1972 a, b; Gwinner, 1973; Gwinner & Dorka, 1976; Gwinner, 1977) emphasizes the probability that mechanisms controlling annual cycles have evolved independently among birds many times.

A primary effect of increasing day length is an increase in the release of gonadotropic hormones and thus gonadal growth. Luteinizing hormone (LH) stimulates the testes to secrete testosterone (Brown et al., 1975; Maung & Follett, 1977), which in conjunction with follicle stimulating hormone (FSH), stimulates and maintains spermatogenesis (Brown & Follett, 1977; Desjardins & Turek, 1977).

If male White-crowned Sparrows previously held on short day lengths (8 L:16 D) are transferred to long days (20 L:4 D) there is a 10—20 fold increase in the plasma level of immunoreactive luteinizing hormone (irLH) within 3—5 days remaining at a maximum throughout the period of testicular growth (Follett et al., 1975). Plasma levels of testosterone and DHT begin to increase by day 20 and reach a maximum at day 30—35 as the logarithmic phase of testicular growth comes to an end (Lam & Farner, 1976). A circadian function in photosensitivity has been demonstrated in this species (Follett et al., 1974) with the photoinducible phase, as far as LH secretion is concerned occurring between 12 and 20 hours after dawn. The plasma levels of LH and

Department of Zoology, University of Washington, Seattle, Washington 98195, U.S.A.

testosterone in males exposed to natural day lengths in Seattle begin to increase in February and reach maxima in late May and early June (MATTOCKS et al., 1976; F. LAM & D. S. FARNER, unpublished).

In captive male White-crowned Sparrows gonadal growth is quantitatively and qualitatively similar to that in the field, but in females, ovarian growth rarely progresses to the phase of yolk deposition. Thus, one is faced with the problem of the significance of temporal changes in plasma levels of hormones in captive birds in comparison with their conspecifics in the field. Photoperiodic mechanisms are sufficient and essential for the initiation of gonadal growth, but at least in females, the presence of a mate with suitable territory for nest sites appears to be necessary for the final maturation of the ovary (KING et al., 1966; FARNER & LEWIS, 1971). Several other factors may also be involved. For reviews of proximate and ultimate factors affecting the fine tuning of breeding cycles see IMMELMANN, 1973; FARNER & FOLLETT, 1978.

Field studies

Recently we (WINGFIELD & FARNER, 1976) described techniques for the procurement of serial blood samples from individual birds in the field. These techniques have now been applied to two taxa of White-crowned Sparrow.

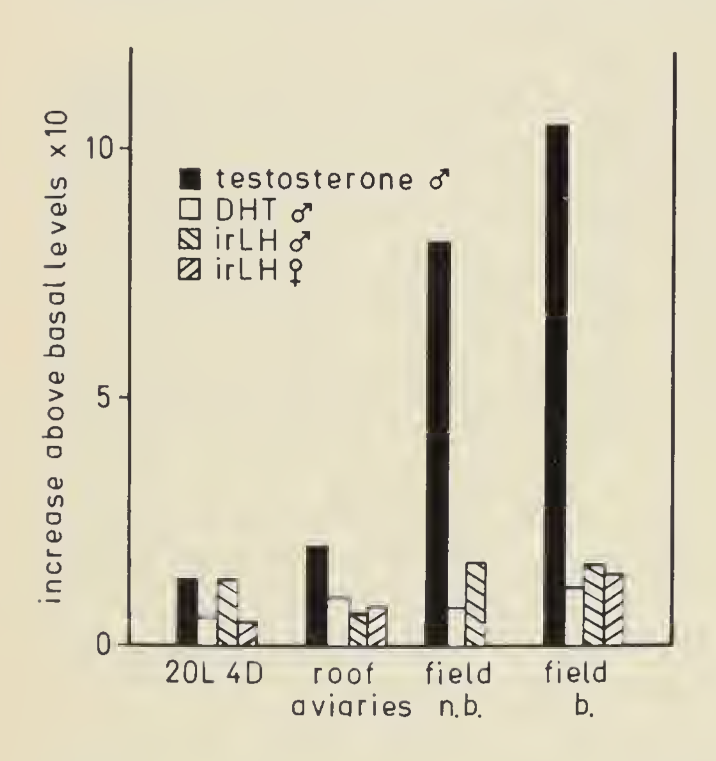


FIGURE 1. Increase in plasma levels of hormones above basal in captive and feral *Z. l. gambelii* during a gonadal cycle. These increases are expressed as the ratio of the maximum plasma level to the minimum plasma level measured throughout a cycle. Data are taken from FOLLETT et al., 1975; LAM & FARNER, 1976 and unpublished; MATTOCKS et al., 1976; WINGFIELD & FARNER, 1977, 1978 a, b and unpublished.

b. — breeding males
n.b. — non-breeding males

In males of the long distance migrant *Z. l. gambelii,* plasma irLH and androgen levels begin to increase in late winter and early spring. As day length increases and migration ensues these levels increase further to maxima in late May and early June when birds are on their breeding territories in central Alaska and courtship and nesting activities are in progress (WINGFIELD & FARNER, 1978 a). A similar trend is seen in males of the short distance migrant *Z. l. pugetensis* that breeds in the Puget Sound area, although courtship and nesting activities begin a full month earlier in late April and early May (WINGFIELD & FARNER 1977, 1978 b).

As testosterone has been implicated in the control of territorial and sexual behavior (e.g. LOFTS & MURTON, 1973), high plasma levels during the period of courtship and

establishment of territory are not surprizing. In Figure 1 it can be seen that the high levels of testosterone in the plasma of *Z. l. gambelii* in the field far exceed those measured in birds in captivity. Testosterone levels in field birds increase substantially more than those in birds with an artificially induced cycle on 20 L: 4 D or in those held in outdoor aviaries ($p > 0.001$). Levels in non-breeding males in the field also increase in a manner similar to that in breeding males. These non-breeding males hold territories but are without mates. The plasma levels of irLH and DHT do not differ so dramatically but do tend to be higher in feral individuals. The lower plasma testosterone levels in males in the laboratory may be a result of the stress of captivity even though testicular growth is qualitatively and quantitatively similar in captive and free living birds. It is also possible that the higher levels in feral birds are the result of other non-photoperiodic factors imparted by the natural environment.

Factors other than day length

As incubation ensues plasma levels of irLH decrease with an accompanying precipitous decline in the plasma levels of testosterone. In *Z. l. gambelii* these levels are near basal by the time that young are being fed (WINGFIELD & FARNER, 1978 a) whereas in the double-brooded *Z. l. pugetensis* the decline in irLH and testosterone during the incubation of the first clutch is not as great. These lower levels of testosterone, still over 10 times greater than basal, may be involved in the maintenance of a territory and pair bond through to courtship and nesting for the second brood. There is no second increase in testosterone despite a second, smaller increase in irLH. During incubation of the second clutch, in this population the final clutch, plasma levels of irLH and testosterone decline to basal values as in the single-brooded *Z. l. gambelii* (WINGFIELD & FARNER, 1977; 1978 b).

Such a decrease in plasma testosterone during incubation may be adaptive in reducing the singing frequency and aggressive behavior in males with an established territory in sufficient time to begin feeding young that hatch 12 to 14 days thereafter (see WINGFIELD & FARNER, 1978 a). In addition the visual and tactile stimuli provided by nest and eggs or young may induce parental type behavior, possibly through the action of prolactin which in turn depresses the secretion of gonadotropin and testosterone (see LEHRMAN, 1961).

We have additional evidence from renesting *Z. l. gambelii* that factors other than day length affect secretion of irLH and testosterone. This form is single-brooded but capable of renesting if the first clutch or brood is lost sufficiently early in the season, i.e. before the onset of photorefractoriness. When renesting both plasma levels of irLH and testosterone increase (Table 1) concomitantly with the return of testis weight to maximum and an increase in singing frequency and courtship behavior. As all birds in the immediate area, whether renesting or not, are subject to the same day length, temperature, rainfall and availability of food then it seems that the stimulus for these increases in irLH and testosterone may be provided by the mate. When the clutch or brood is lost the stimuli for parental behavior and the inhibitory effect on the secretion of gonadotropins (see LEHRMAN, 1961) in the female are lost, and since the daily photoperiod is still long, she begins anew the rapid final maturation stage in ovarian growth. Males do not incubate but do help to feed young, therefore such a mechanism might

operate in males also. However, as estrogen levels increase in females (see WINGFIELD & FARNER, 1978 a, b) she begins courtship posturing, thus providing additional visual, and possibly auditory and tactile, stimuli to the male which may cause increased secretion of irLH and testosterone and a return of testis weight to maximum.

It should be also noted that this second peak in plasma testosterone (Table 1) is similar to the level maintained between broods in *Z. l. pugetensis* (WINGFIELD & FARNER 1978 b) and significantly less ($p < 0.05$) than the first. As the same pairs remain mated and on the same territory when renesting it is thought that as in *Z. l. pugetensis* this lower level of testosterone is sufficient to maintain the pair bond and territorial and sexual behavior.

TABLE 1: Plasma hormone levels in renesting male *Z. l. gambelii* sampled in the Fairbanks region of Alaska

hormone	nesting for first clutch	loss of clutch: incubation	loss of clutch: feeding young	renesting
irLH	5.02 ± 0.27	3.54 ± 0.24	3.23 ± 0.38	6.16 ± 0.75
testosterone	4.18 ± 0.49	0.65 ± 0.11	0.45 ± 0.21	1.88 ± 0.56
DHT	0.45 ± 0.08	0.13 ± 0.02	0.15 ± 0.03	0.20 ± 0.04

All figures are means ± standard error.
[1] irLH = immunoreactive luteinizing hormone.

There is evidence of a possible mechanism by which such information may regulate hormone titers. YOKOYAMA & FARNER (1976) have shown that inhibitory information may be mediated via the eyes in captive female *Z. l. gambelii* depressing plasma irLH and inhibiting the final maturation phase of the ovary. Whether or not such a mechanism is in operation in males remains to be determined.

Acknowledgements

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The Role of the Testes in the Initiation and Maintenance of Photorefractoriness

P. J. Sharp

Introduction

Many birds stop breeding in the summer even though they are exposed to photoperiods which are longer than those which stimulated breeding in the spring. Such birds are termed, 'photorefractory' because reproductive activity is not maintained by long photoperiods. In male birds (data for females are more limited), the development of photorefractoriness is associated with a fall in the concentrations of plasma luteinizing hormone (LH), follicle stimulating hormone (FSH) and testosterone (e.g. Garnier, 1971; Temple, 1973; Wilson & Follett, 1974; Haase et al., 1975; Sharp et al., 1975; Balthazart & Hendrick, 1976; Mattocks et al., 1976). These observations suggest that the testes regress in photorefractory birds because of a reduction in the secretion of LH and FSH and not because there is an internal annual rhythm of testicular activity (Marshall, 1951) or a selective depression of FSH secretion (e.g. Murton, 1975). Photorefractoriness is also unlikely to be due to an 'exhaustion' of the pituitary gland, since LH release occurs in response to injections of synthetic LH-releasing hormone (LH-RH) in photosensitive, photorefractory and breeding birds (e.g. Sharp, 1978). The reduction of gonadotrophin secretion in photorefractory birds thus appears to be due to a reduction in the secretion of LH-RH by the hypothalamus.

Two general approaches have been adopted to explain why the secretion of LH-RH is reduced in photorefractory birds. One starts with the premise that, since endogenous rhythms are involved in many physiological functions, including the photoperiodic induction of testicular growth (e.g. Farner, 1975), they are also responsible for the regulation of testicular regression. The other is derived from the premise that, since changes in hypothalamic sensitivity to the negative feedback action of steroids are thought to be involved in the initiation of puberty (e.g. Davidson, 1974) and in seasonal breeding in mammals (e.g. Pelletier & Ortavant, 1975 b; Legan et al., 1977), an increase in the sensitivity of the hypothalamus to the inhibitory effects of steroids may cause photorefractoriness in birds. Other papers in this volume deal with aspects of the role of endogenous (circadian and circannual) rhythms in seasonal breeding; in this paper, attention is focused on some experiments in which the role of the testes in the regulation of photorefractoriness has been investigated.

The role of the photoperiod and steroid feedback in seasonal breeding

If changes in the sensitivity of the hypothalamus to the negative feedback effects of gonadal steroids are responsible for the regulation of seasonal breeding, then the inhibitory or stimulatory effects of decreasing or increasing photoperiods on gonadotrophin release must be mediated via the gonads. It follows that in the absence of the gonads the concentration of plasma LH will be elevated and similar in animals exposed

Agricultural Research Council's Poultry Research Centre, King's Buildings, Edinburgh EH9 3JS, United Kingdom.

to stimulatory or inhibitory photoperiods. This prediction has been confirmed in ovariectomised ewes (LEGAN et al., 1977) but not in rams (PELLETIER & ORTAVANT, 1975 a), quail (GIBSON et al., 1975) or tree sparrows (WILSON & FOLLETT, 1977). In castrated rams, quail and sparrows, the concentration of plasma LH is higher in animals exposed to stimulatory photoperiods than in those held on inhibitory photoperiods. However, in various species, including ducks (GOGAN & KORDON, 1964) rams (PELLETIER & ORTAVANT, 1975 b) and quail (DAVIES et al., 1976), there is evidence that the hypothalamic-pituitary unit is less sensitive to steroid negative feedback under stimulatory photoperiods than under non-stimulatory photoperiods. These observations lead to the conclusion that seasonal breeding may be controlled by two mechanisms: the relative importance of either mechanism may vary between the sexes and between species. The first mechanism involves a direct effect of the photoperiod on gonadotrophin release and the second involves an effect of the photoperiod on the sensitivity of the hypothalamic-pituitary complex to inhibitory steroids (Fig. 1). Both mechanisms are envisaged as being mediated via endogenous (circadian or circannual) rhythms (Fig. 1).

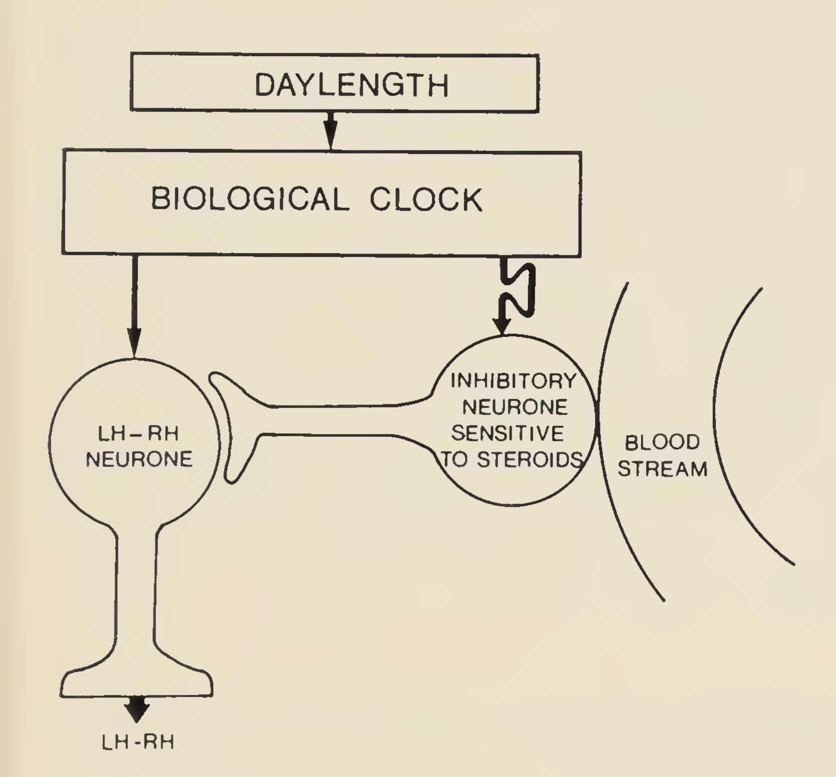


FIGURE 1. A diagrammatic illustration of the principal mechanisms which have been suggested to be involved in the regulation of seasonal breeding. Seasonal changes in the photoperiod are thought to influence directly (straight arrow) the activity of LH-RH neurones and to modulate indirectly (bent arrow) the sensitivity of the hypothalamus to the negative feedback action of gonadal steroids.

The role of the testes in the maintenance of photorefractoriness

In order to explain the physiological basis of photorefractoriness in terms of the mechanisms illustrated in Fig. 1 it is suggested that the direct stimulatory effect of long photoperiods on the activity of LH-RH neurones is counteracted by the inhibitory effect of neurones sensitive to steroids. It follows that the sensitivity of the inhibitory neurones to steroid feedback increases as a result of exposure to long photoperiods. This increased sensitivity is thought to develop progressively during the course of the breeding season and may be due to an interaction with hormones secreted as a result of photostimulation. The effect of the photoperiod on the sensitivity of inhibitory neurones to steroid feedback is therefore believed to be indirect (Fig. 1). A test of this hypothesis would be to show that in photorefractory birds, the concentrations of plasma gonadotrophins are high in the absence of inhibitory steroids in the blood.

Since testicular and adrenal steroids inhibit the secretion of LH in birds (Wilson & Follett, 1975, Davies et al., 1976; Yokoyama, 1977), removal of all inhibitory steroids can only be achieved by removing or inactivating both the testes and adrenal glands. At the time of writing the result of such an experiment has not been reported. However, the effect of removing the testes on the concentration of plasma LH has been investigated in photorefractory canaries (Nicholls & Storey, 1976) and red grouse (Sharp & Moss, 1977). The resulting observations are conflicting because in photorefractory canaries maintained on a long photoperiod the concentration of plasma LH remained low after castration whereas in photorefractory grouse maintained on a long photoperiod, castration caused a steep increase in the concentration of this hormone. This species difference may be explained by supposing that adrenal steroids play a more important role in the maintenance of photorefractoriness in canaries than they do in grouse. The observation that the adrenals nearly double in mass in photostimulated intact and castrated sparrows (Stetson & Erickson, 1971) further supports the view that, in finches, seasonal changes in adrenal activity could play a role in the maintenance of photorefractoriness.

Photorefractoriness can not be due to a failure of the biological clock to measure time since photorefractory birds respond differently to long or short photoperiods. Thus the concentration of plasma LH increases steeply in photorefractory castrated red grouse (Sharp & Moss, 1977) and willow grouse (Stokkan & Sharp, unpublished) maintained on a long photoperiod but fails to increase (willow grouse) or increases slowly (red grouse) when the birds are maintained on a short photoperiod. Photorefractory canaries can also distinguish between long and short photoperiods since photosensitivity is regained if the birds are held on short photoperiods but not if they are kept on long photoperiods (Nicholls & Storey, 1976).

These observations are consistent with the hypothesis that photorefractory birds are still aware of long photoperiods as indicated in Fig. 1 but are unable to respond because of the inhibitory feedback effects of testicular and adrenal steroids. In the finches, but not in grouse, the testes do not appear to be essential for the maintenance of photorefractoriness.

As mentioned previously the sensitivity of the hypothalamus to steroid feedback may increase progressively during the breeding season because of an interaction with hormones secreted as a result of photostimulation. There are two reports which suggest that one such hormone could be thyroxine. Thus in ducks, the concentration of plasma thyroxine is elevated during the photorefractory period (Astier et al., 1970) and in starlings photorefractoriness does not develop if the birds are thyroidectomized before exposure to long photoperiods (Wieselthier & van Tienhoven, 1972). Our studies on Mallard drakes (Sharp & Klandorf, unpubl.) show that the concentration of plasma thyroxine increases at the end of breeding period after the concentrations of plasma LH and testosterone have fallen (Sharp & Klandorf, unpubl.). It is therefore doubtful if increased thyroid activity plays a primary role in the initiation of photorefractoriness.

The role of the testes in the initiation of photorefractoriness

One of the arguments against the view that an increase in hypothalamic sensitivity to steroid feedback is responsible for the development of photorefractoriness is the obser-

vation that castrated finches (e.g. STETSON & ERICKSON, 1971; WILSON & FOLLETT, 1974; MATTOCKS et al., 1976) and castrated grouse (SHARP et al., 1975; STOKKAN & SHARP, unpubl.) become photorefractory. However, as mentioned previously this argument can not be accepted without reservation until it can be shown that adrenalectomized-gonadectomized birds also become photorefractory.

In all the finch studies mentioned above, as judged by the time taken for the concentrations of plasma LH to begin to fall, the onset of photorefractoriness began in castrated birds at about the same time as in the intact controls. This observation suggests that photorefractoriness is initiated by a mechanism which is independent of the testes. Subsequent studies have shown that this inference does not hold for willow grouse (STOKKAN & SHARP, unpubl.) or for canaries (STOREY et al., unpubl.). In photosensitive willow grouse the concentration of plasma LH increased and returned to a base-line over a period of 67 days after castration and transfer from a non-stimulatory (8L:16D) to a stimulatory photoperiod (8D: 16L). Plasma LH levels in intact control grouse were still elevated 67 days after transfer to the stimulatory photoperiod. In canaries transferred from a non-stimulatory photoperiod (8L: 16D) to a marginally stimulatory photoperiod (11L: 13D) or to a highly stimulatory photoperiod (20L: 4D), as judged by changes in the concentration of plasma LH, castrated birds became photorefractory more quickly than intact controls. It took 95 and 67 days respectively for castrated canaries held on photoperiods of 11L: 13D and 20L: 4D to become photorefractory. The corresponding figures for the intact control birds were >230 days for birds on 11L: 13D and 130 days for birds on 20L: 4D. These observations show that both the length of the photoperiod and the secretions of the testes can play a role in the regulation of the onset of photorefractoriness. This dual mechanism may be important in species like the canary which have a relatively long breeding season. In species like Tree Sparrows (WILSON & FOLLETT, 1974) and White-crowned Sparrows (MATTOCKS et al., 1976), in which the breeding season is short, this effect of the testes may have no adaptive significance and be suppressed.

Conclusions

Although the evidence is still fragmentary, it seems that in some species the testes play a role in the development and maintenance of photorefractoriness. In photorefractory grouse the concentration of plasma LH is kept depressed by testicular hormones while in the canary, the testes play a role in the timing of the onset of photorefractoriness.

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Die endogene Steuerung der Jahresperiodik: Eine kurze Übersicht

Peter Berthold

Einführung

Das Studium der endogenen Steuerung der Jahresperiodik hat in den letzten Jahren beträchtliche Fortschritte gemacht. Im folgenden wird eine kurze Übersicht über die bisher erzielten Ergebnisse gegeben, die eine allgemeine Einschätzung des Phänomens erlauben und Anregungen für weiterführende Untersuchungen geben soll.

Nachweise circannualer Rhythmik

Die besten Beweise für die endogene Steuerung jahresperiodischer Vorgänge sind sichere Nachweise circannualer Rhythmen. Tab. 1 faßt die bisher erzielten Nachweise circannualer Periodik zusammen. Circannuale Rhythmik konnte inzwischen bei insgesamt 13 Vogelarten aus 6 verschiedenen Familien und für 4 verschiedene jahresperiodische Vorgänge nachgewiesen werden.

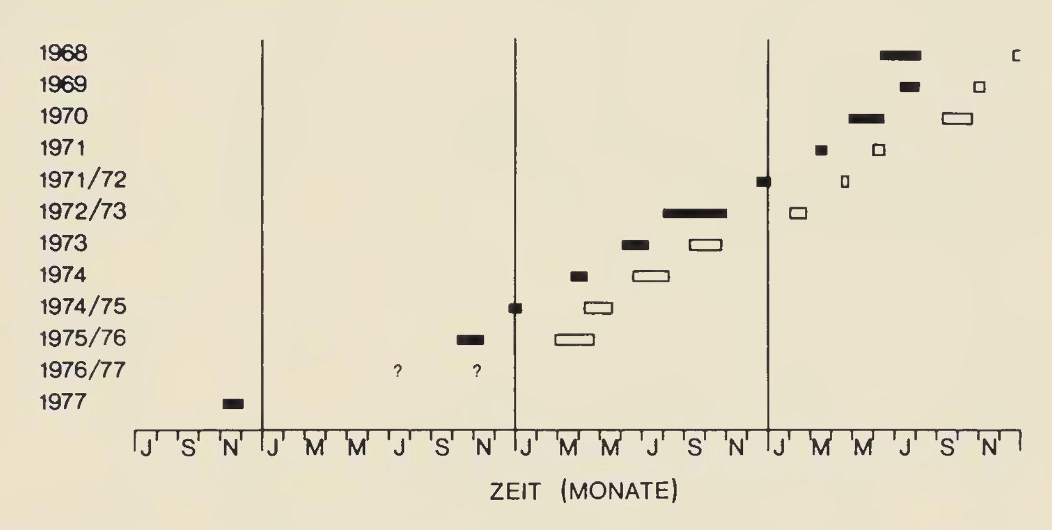


Abb. 1: Circannuale Mauserperiodik einer handaufgezogenen *Sylvia borin* bei zehnjähriger Haltung in konstanten Bedingungen (LD 10 : 14). Zur Veranschaulichung des Freilaufens der Periodik ist das Kalenderjahr 3,5mal nebeneinander aufgetragen. Schwarze Balken: „Sommer"-Mauser; weiße Balken: „Winter"-Mauser; ?: vermutliche Mauserzeit ohne Mauser (Berthold unveröffentlicht).

Beispiele circannualer Rhythmen

Inzwischen gelangen einige besonders überzeugende und aufschlußreiche Nachweise circannualer Rhythmen, von denen einer in Abb. 1 dargestellt ist. Eine Gartengrasmücke *Sylvia borin* zeigte in konstanten Versuchsbedingungen eine freilaufende Mauserperiodik über die Dauer von zehn Kalenderjahren. Mit einer durchschnittlichen Periodenlänge von 9,7 Monaten verfrühten sich die Beginne der einzelnen Mausern von Jahr zu Jahr fortlaufend, so daß der Vogel in den ersten 7 Kalenderjahren 8 subjektive Mauserzyklen und mit seiner Mauserperiodik insgesamt fast dreimal das ganze Kalenderjahr durchlief. 1976 und 1977 mauserte der Vogel jeweils nur einmal. Die 1977er Mauser liegt jedoch derart in der Verlängerung der Sequenz der „Sommer"-

Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell, Bundesrepublik Deutschland.

Tabelle 1: Nachweise circannualer Rhythmen bei Vögeln (nach BERTHOLD 1974 a und GWINNER 1975, vervollständigt)

Art	Bedingungen (LD)	periodische Vorgänge	maximale Versuchs-dauer in konstanten Bedingungen (Monate)	maximale Anzahl gemessener Zyklen	Perioden-länge (Monate)[1]	Untersucher, Jahr der Publikation[2]
Phylloscopus trochilus	12:12	Mauser, Zugunruhe	28	3	9, 11,8	GWINNER 1967
Sylvia atricapilla *S. borin*	10:14 12:12 16: 8	Körpergewicht, Mauser, Zugunruhe, Gonadenzyklus	120	9	10,5 10,6	BERTHOLD et al. 1971
Sturnus vulgaris	12:12	Hodengröße, Mauser	43	3	10, 12,5	SCHWAB 1971, GWINNER 1977a
Sylvia cantillans	10:14	Körpergewicht, Mauser, Zugunruhe	19	2	11,3	
S. melanocephala	10:14	Mauser, Zugunruhe	19	2	10,5	BERTHOLD 1973
S. sarda	10:14	Mauser, Zugunruhe	19	2	10,4	
S. undata	10:14	Mauser, Zugunruhe	19	2	10,8	
Parus cristatus	10:14	Mauser	22	2	10,4	BERTHOLD 1973 und unveröffentlicht
Fringilla coelebs	12:12 20: 4	Mauser, Körpergewicht, Gonadenzyklus	34	2	8—13	DOLNIK 1974
Zonotrichia albicollis	16:10	Mauser			13,5	MEIER 1976
Loxia curvirostra	12:12	Mauser, Körpergewicht, Hodengröße	47	4	10,6	BERTHOLD 1977 c und unveröffentlicht
Passer montanus	10:14	Hodengröße	38	2	8—15	BERTHOLD unveröffentlicht

[1] Einzel-, Mittel- sowie Näherungswerte; Näheres s. GWINNER 1975, BERTHOLD 1974 a und Originalarbeiten
[2] Erstpublikation für die jeweilige Art

Mausern, daß sie trotz ausgefallener Mausern wie das Ergebnis einer weiterhin wirkenden circannualen Rhythmik erscheint.

Ähnliche Ergebnisse liegen für eine Mönchsgrasmücke *S. atricapilla* und für das Körpergewicht der Gartengrasmücke vor (Berthold unveröffentlicht). Diese Daten lassen schließen, daß die circannuale Periodik dieser Vögel ohne Zweifel endogene, also vom Organismus selbst erregte Schwingung ist, die die untersuchten Vorgänge wohl lebenslang zu steuern vermag.

Die endogene Steuerung des Zuges

Der Zug ist derjenige jahresperiodische Vorgang, dessen endogene Steuerung am eingehendsten untersucht wurde. Die endogene Steuerung des Zuges wurde in letzter Zeit mehrfach zusammenfassend behandelt (Berthold 1977 a, 1978, Gwinner 1977 a), so daß hier nur die wesentlichen Ergebnisse kurz aufgeführt zu werden brauchen.

Spontaner Körpergewichtsanstieg in der Zugdisposition und spontaner Gewichtsabfall durch Depotfettbildung bzw. -abbau bei unter konstanten Bedingungen aufgezogenen Jungvögeln sind für 4 Arten bekannt. Für dieselbe Gruppe von Vögeln sind spontanes Auftreten und Beendigung der Zugunruhe zur Zeit des ersten Wegzugs bei 6 Arten nachgewiesen. Bei 3 bzw. 6 Arten ist erwiesen, daß Zugdisposition und Zugaktivität aufgrund von circannualer Rhythmik regelmäßig wiederkehren können (Tab. 1). Von 4 Arten ist bekannt, daß an der Steuerung der Nahrungswahl im Jahresverlauf (Art der Nahrung und Menge betreffend) endogene Faktoren wesentlich beteiligt sind. Für eine Art ist — durch eine Serie von Versuchen — belegt, daß die zeitlichen Muster sowohl der Zugdisposition (Depotfettanlagerung) als auch der Zugunruhe streng endogen kontrolliert werden. Bei mindestens 7 Arten konnte gezeigt werden, daß Wahl und/oder Beibehaltung der art- oder populationsspezifischen Zugrichtung angeboren sind. Bei einer Art ist inzwischen auch nachgewiesen, daß selbst Änderungen der Zugrichtung während des Zugs endogen programmiert sein können. Für eine Art ist sicher, daß populationsspezifische Charakteristika sowohl der Jugendentwicklung in Anpassung an das Zugverhalten als auch des Zugverhaltens selbst endogen gesteuert werden und offensichtlich genetisch fixiert sind (Berthold 1977 b). Bei 2 Artengruppen ließ sich zeigen, daß die endogen produzierten Zugunruhemengen eng positiv mit der zurückzulegenden Zugstrecke korreliert sind. Aus diesen Daten wurde abgeleitet, daß Zugvögel art- und populationsspezifische Winterquartiere mit Hilfe angeborener Zugrichtungen und endogener Zugzeitprogramme auffinden könnten (Vektor-Navigations-Hypothese).

Die endogene Steuerung der Jahresperiodik weniger ausgeprägter Zugvögel und Standvögel

In der Diskussion um Verbreitung und Bedeutung der circannualen Periodik wurde u. a. argumentiert, sie könnte ein Spezifikum bestimmter Gruppen, zum Beispiel stark ausgeprägter Zugvögel, sein, denen komplizierte und besonders präzise Jahresperiodik abverlangt wird (z. B. Gwinner 1971, Berthold 1974 a, Farner 1975). Um diese Vorstellung zu testen, untersuchten wir wenig ausgeprägte Zugvögel und Standvögel auf circannuale Rhythmik.

Drei wenig ausgeprägt ziehende Grasmückenarten zeigten circannuale Periodik der Mauser und der Zugunruhe (z. B. BERTHOLD 1974 b u. Tab. 1). Beim Invasionsvogel *Loxia curvirostra* steuert circannuale Rhythmik Körpergewichtsänderungen (BERTHOLD 1977 c), die Mauser (nachgewiesen bei bis zu 4jähriger Haltung, mit einer durchschnittlichen Periode von 10,6 Monaten, n = 5; BERTHOLD unveröffentlicht u. Tab. 1) und mindestens zum Teil den Gonadenzyklus: Bei einigen ♂ wurden bei bis zu 4jähriger Haltung circannualer Rhythmen der Hodengröße beobachtet, bei anderen wiederholte spontane Änderungen der Hodengröße (BERTHOLD unveröffentlicht u. Tab. (1). *Parus cristatus,* einer der ausgeprägtesten Standvögel in seinem gesamten europäischen Verbreitungsgebiet, zeigte klare circannuale Rhythmik der Mauser bei allen Vögeln einer Versuchsgruppe (Abb. 2, durchschnittliche Periode 10,4 Monate). Beim Standvo-

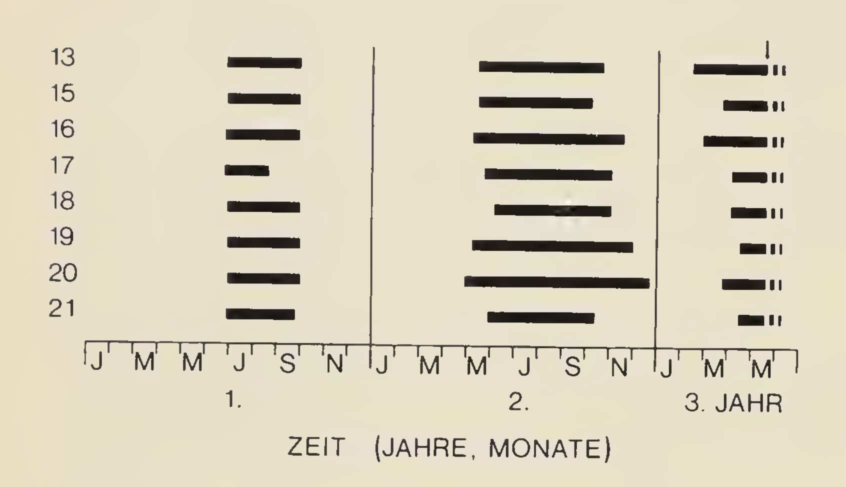


Abb. 2: Circannuale Mauserperiodik von 8 handaufgezogenen *Parus cristatus* (im LD 10:14) Zahlen: Nummern der Versuchsvögel; Pfeil: Ende des Versuchs (BERTHOLD, unveröffentlicht).

gel *Passer montanus* ließ sich circannuale Rhythmik der Hodengröße bei zwei ♂ nachweisen (Tab. 1). Andere ♂ und auch ♀ zeigten bei bis zu 3jähriger Haltung in konstanten Bedingungen mehrfach spontane Gonadengrößenänderungen in zum Teil erheblichem Umfang (BERTHOLD unveröffentlicht).

Die Synchronisation circannualer Rhythmen

Die Periode von Jahresrhythmen beträgt unter natürlichen Bedingungen — zumindest im Mittel — häufig genau ein Jahr, wohingegen die solchen Rhythmen zugrundeliegende circannuale Periodik regelmäßig mehr oder weniger deutlich von 12 Monaten abweicht. Demnach müssen Umweltfaktoren — sogenannte Zeitgeber — existieren, die die endogene Periodik mit der Umwelt synchronisieren (z. B. ASCHOFF 1960). Aus der Tatsache, daß bei vielen Vogelarten Änderungen der Tageslichtdauer den stärksten bekannten Einfluß auf die Jahresperiodik haben, wurde u. a. geschlossen, daß die Photoperiodizität wesentlichster Zeitgeber sein müßte (Übersicht: z. B. GWINNER 1977b). Inzwischen ist bei Vögeln die Zeitgeberfunktion der Photoperiodizität in drei Fällen erwiesen: Bei *Sturnus vulgaris* konnte GWINNER (1977c) zeigen, daß die Photoperiode die endogenen Mauser- und Gonadenzyklen synchronisiert, und zwar auch dann, wenn fünf Photoperiode-Zyklen pro Jahr gegeben werden und die Zeitgeberperiode damit nur 2,4 Monate beträgt. *Sylvia borin* und *melanocephala* folgten mit ihren Mauser- und Zugunruhe-Zyklen, wenn zwei Photoperiode-Zyklen pro Jahr geboten wurden. *S. borin* durchlief in dieser Zeit jedoch nur einen Körpergewichtszyklus (BERTHOLD unveröffentlicht).

Gwinner (1977 c) fand bei seinen Untersuchungen an *Sturnus vulgaris,* daß sich mit abnehmender Zeitgeberperiode die Phasenbeziehungen zwischen Mauser- und Gonadenrhythmik sowie der Photoperiode systematisch änderten. Diese Festellung stimmt überein mit Voraussagen der allgemeinen Schwingungslehre und spricht dafür, daß circannuale Rhythmen wie Oszillatoren im technischen Sinn betrachtet werden können.

Schlußbetrachtung

Die vorliegende Übersicht zeigt: Circannuale Rhythmen sind keine Spezialmechanismen einer bestimmten Vogelgruppe oder einiger weniger systematischer oder ökologischer Gruppen, sondern sind vielmehr in einer ganzen Reihe von Familien und ökologischen Gruppen — vom ausgeprägten Zugvogel über Invasionsvögel bis hin zum reinen Standvogel — nachgewiesen. Die große und ständig zunehmende Anzahl der Beinahe-Nachweise circannualer Rhythmen sowie weiterer starker Hinweise darauf (z. B. Berthold 1974 a, Gwinner 1975, 1976) läßt erwarten, daß sich circannuale Periodik als wesentlich weiterverbreitet erweisen wird als bisher nachgewiesen ist. Ob sich die Ansicht von Murton & Westwood (1977) bestätigen wird, nach der wahrscheinlich die meisten, wenn nicht alle Vogelarten offenbar autonome Jahresrhythmen entwickeln, wenn sie unter entsprechenden Lichtbedingungen gehalten werden, ist offen. Bei einigen Arten, bei denen für einzelne jahresperiodische Funktionen bislang auch bei Nachsuche in verschiedenen Bedingungen keine circannuale Periodik gefunden werden konnte (z. B. für Gonadenzyklen bei *Zonotrichia,* Sansum & King 1976, Mauserzyklen bei *Passer montanus,* Berthold unveröffentlicht) ist vorläufig nicht zu entscheiden, ob die genannten Vorgänge nicht endogen gesteuert werden oder ob bei diesen Arten bislang nur die für den Nachweis circannualer Rhythmen möglicherweise erforderlichen speziellen Bedingungen (z. B. Schwab 1971, Berthold 1974 a) noch nicht getestet wurden. Daß manche Arten circannuale Periodik in einem weiten Feld verschiedener konstanter photoperiodischer Bedingungen zeigen (z. B. Sylviiden, Berthold 1974 a), andere in einer Reihe von verschiedenen konstanten Bedingungen kaum oder gar nicht (*Zonotrichia, Passer,* l.c.) spricht u. U. für die Ansicht einiger Autoren, z. B. Farner (1975): daß hinsichtlich der endogenen und exogenen Steuerung der Jahresperiodik von Vögeln ein Spektrum von Typen bestehen könnte, die im einen Extrem selbsterregte Jahresperiodik besitzen, im anderen Steuersysteme, die nach 1—2 Zyklen ausdämpfen und von außen — durch die Photoperiodizität — wieder angestoßen werden müssen. Ob nur bei ersteren innere Jahreskalender für die Steuerung der Jahresperiodik so wichtig sind wie Umweltrhythmen (Gwinner 1976) und welche Rolle endogene Faktoren bei der möglichen zweiten Gruppe von Vögeln letztlich spielen, zum Beispiel in Form von „endogenen circannualen Perioden" (Farner 1975), ist vorerst ebenfalls nicht zu beurteilen. Für eine zukünftige allgemeinere und genauere Beurteilung des Phänomens der endogenen Steuerung der Jahresperiodik halte ich drei Vorhaben für besonders erfolgversprechend: Die Untersuchung weiterer systematischer und ökologischer Gruppen und das detaillierte Studium von Arten der beiden Enden des vermuteten Spektrums unter möglichst vielen verschiedenen konstanten Bedingungen.

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The Role of the Pineal Gland in the Regulation of Annual Reproductive Cycles in Birds and Mammals: A Comparative Approach

Fred W. Turek

Introduction

The pineal gland is involved in the photoperiodic control of the reproductive cycle in many mammals. In contrast, there is very little evidence to suggest that the pineal gland plays an important role in the photoperiodic control of reproduction in birds. We have sought to re-examine the role of the avian pineal gland in photic-induced changes in neuroendocrine-gonadal function because of the following three observations: 1) Both pinealectomy and melatonin treatment interfere with circadian rhythmicity in birds; 2) Photoperiodic time measurement in birds involves the circadian system; 3) Pineal-mediated effects upon the mammalian reproductive system are influenced by the photoperiod and the circadian system. Our preliminary data suggest that the pineal gland, as part of the circadian system responsible for photoperiodic time measurement, may be involved in the avian photosexual response.

Pineal gland: Role in reproduction and circadian organization

Pinealectomy, or treatment with the putative pineal hormone melatonin, alters the response of the neuroendocrine-gonadal axis to photoperiodic information in a number of different mammalian species (Hoffmann & Küderling, 1975; Reiter et al., 1975; Turek et al., 1975; Thorpe & Herbert, 1976). Both progonadal and antigonadal effects of pinealectomy and melatonin administration have been observed in mammals, and one factor which influences the response to such treatment appears to be the length of the day (Hoffmann & Küderling, 1975; Turek & Losee, 1978). Furthermore, the circadian system has been implicated in pineal-mediated effects on the reproductive system, since daily melatonin injections were found to inhibit neuroendocrine-gonadal activity in the golden hamster only when given at certain times of the day (Tamarkin et al., 1976).

While previous studies indicate that the effect of pinealectomy or melatonin treatment on the avian photosexual response is minimal (Menaker & Oksche, 1974; Turek & Wolfson, 1978), such treatment does lead to pronounced changes in the circadian rhythm of locomotor activity in birds (Gaston & Menaker, 1968). In house sparrows maintained in constant darkness, pinealectomy induces arrhythmicity, and the continuous administration of melatonin alters the free-running period of the activity rhythm (Zimmerman & Menaker, 1975; Turek et al., 1976). It is important to note that pineal-mediated effects on the circadian organization of birds appear to be minimal when birds are maintained under standard laboratory lighting conditions such as LD 12:12 or 8:16 (Binkley et al., 1971; Hendel & Turek, 1978). Previous attempts to examine the role of the pineal gland in the avian photosexual response have involved birds maintained under standard laboratory conditions. A more critical test of the pineal gland's role in avian photoperiodism would be to examine the photoperiodic

Department of Biological Sciences, Northwestern University, Evanston, Illinois 60201, USA

response during exposure to lighting conditions that require an intact pineal gland for normal entrainment to occur.

Circadian organization and the photoperiodic control of reproduction

It is now firmly established that an endogenous circadian rhythm is somehow involved in photoperiodic time measurement in both birds and mammals (HAMNER, 1963; FOLLETT & SHARP, 1969; TUREK, 1972, 1974; ELLIOTT, 1976). Although the exact nature of this involvement is not known, one hypothesis (referred to as the external coincidence model) predicts that photoperiodic induction occurs when light is coincident (or not coincident) with an underlying circadian rhythm of photosensitivity to light (PITTENDRIGH, 1972). Because of the theoretical nature of this rhythm, the circadian rhythm in locomotor activity is often used to monitor the phase relationship between the photosensitivity rhythm and the light cycle.

In a recent study using light-dark cycles of varying periods (T) with photophases of a fixed 3-hour duration, it was found that the circadian cycle in locomotor activity and the photoperiodic sensitivity rhythm appear to be coupled together in House Sparrows (FARNER et al., 1977). The phase-angle difference (Ψ) between the locomotor activity rhythm and the environmental light cycle was observed to increase as a function of T, and furthermore, as T was increased beyond 24 hours, the rate of testicular growth increased as a nonlinear function of Ψ. Since pinealectomized House Sparrows show a different Ψ between the activity rhythm and the Zeitgeber during exposure to very short days (i.e., LD 3:21) than do intact birds (GASTON, 1971), we sought to exploit this difference in the entrainment pattern between pinealectomized and intact birds to determine if the gonadal response during exposure to LD 3:21 would vary between intact and pinealectomized animals.

Fourteen photosensitive House Sparrows captured in the winter of 1978 were maintained on LD 8:16 until March 11. The birds were laparotomized at this time, and all were found to have regressed testes (i.e., estimated paired testicular weight of less than 15 mg.). The birds were then either pinealectomized (Px), or sham-pinealectomized (Sham-Px), and moved to an LD 3:21 light cycle. The birds were housed in individual

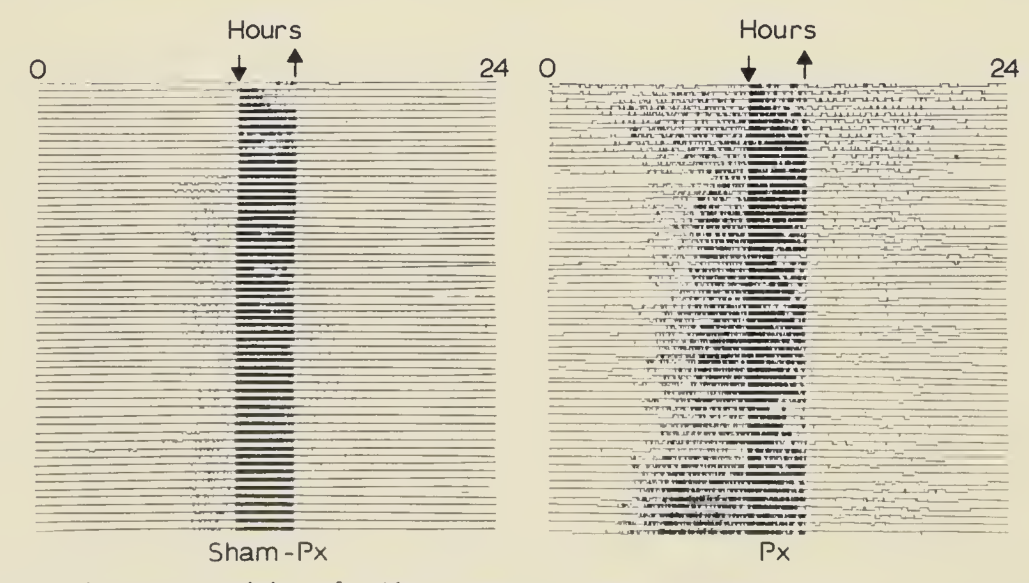


FIGURE 1. Perch-hopping activity of a Sham-Px and a Px male House Sparrow maintained on LD 3:21 for 61 days. Lights on = ↓, lights off = ↑. At the termination of the experiment, the testes of the Sham-Px bird weighed 10 mg, while those of the Px bird weighed 150 mg.

cages and perch-hopping activity was recorded. Sixty-one days later the birds were sacrificed, and the testes were removed and weighed.

In support of previous findings, Px birds tended to entrain to LD 3:21 with a greater phase lead of the onset of light than in intact animals ($.10 > p > .05$). Figure 1 shows the entrainment pattern of a Px and a Sham-Px bird. The small amount of activity observed prior to the onset of light in the intact bird (Fig. 1) might suggest that the true onset of activity may have been masked by the inhibitory effects of the dark period. However, the gonadal response of those birds showing minimal activity prior to the onset of light indicates that the circadian rhythm involved in photoperiodic time measurement was also in a different phase relationship to the light cycle. Testicular weight was correlated ($r = .75$) with the phase angle between the onset of locomotor activity and the onset of light in both Sham-Px and Px birds (Fig. 2). Light falling early in the

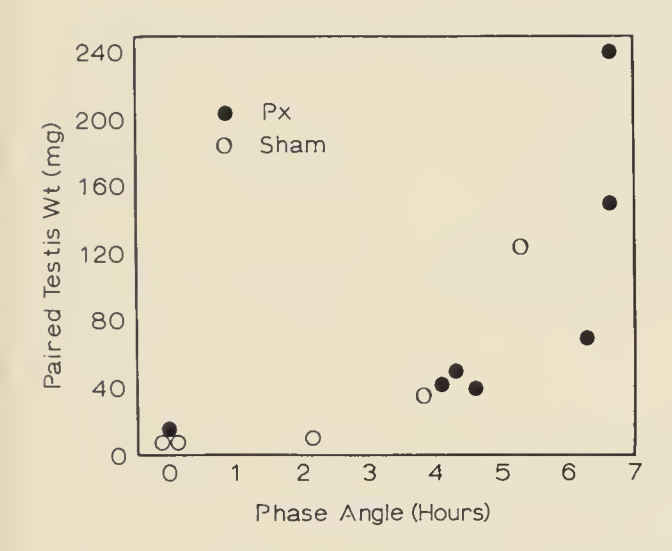


FIGURE 2. Paired testicular weight of individual House Sparrows as a function of the phase angle difference between the onset of activity and the onset of the light during exposure to an LD 3:21 light cycle. Px birds = ●; Sham-Px = ○.

subjective day did not induce testicular growth, whereas light falling later in the day did induce growth. These results are consistent with the hypothesis that the phase relationship between the light-dark cycle and an underlying circadian rhythm of sensitivity to light is responsible for inducing a photoperiodic response in birds (FARNER et al., 1977). Interestingly, light falling between 4—7 hours after the onset of light did induce some testicular growth. Whether this indicates a photosensitive phase that falls in the middle of the subjective day in House Sparrows in the spring of the year, or whether the activity rhythm does not precisely monitor the state of the photosensitivity rhythm remains to be determined.

Because six of the seven Px birds had larger testes than four of the five Sham-Px birds, the differences in testicular weight were found to be significant ($p = .05$) using the Mann-Whitney U-test. In addition, two intact birds died during the course of the study, and both were found to have regressed testes at autopsy. While these data suggest that pinealectomy can alter the entrainment pattern of birds to certain light-dark cycles and thereby alter the photoperiodic gonadal response, further studies involving a larger sample of birds need to be carried out to verify this hypothesis.

At the present time it is not clear why the effects of pinealectomy on circadian organization (and possibly reproductive function) are only manifest in birds maintained in DD or abnormally short light-dark cycles (BINKLEY et al., 1971; GASTON, 1971). Past attempts to evaluate the effect of pinealectomy have been limited to birds maintained

under laboratory lighting conditions that have a very abrupt onset and offset of the light. Aschoff (1965) has demonstrated in birds that twilight plays an important role in establishing the phase relationship between the activity rhythm and the light-dark cycle. Perhaps a more critical examination of the function of the pineal gland would be to assess the entrainment and reproductive response of birds exposed to natural lighting conditions which involve a gradual transition from day to night and night to day.

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SYMPOSIUM ON ECOLOGICAL ASPECTS OF BIORHYTHMS

6. VI. 1978

CONVENER: DAVID W. SNOW

Aspects of Biorhythms in the Budgerigar *Melopsittacus undulatus* (SHAW), a Parrot of Inland Australia

EDMUND WYNDHAM

Introduction

The Budgerigar has been cited as an example of a bird adapted to live in the arid interior of Australia (SERVENTY, 1971). Stress has been placed on its nomadic movements; the need to breed quickly, at any time of the year and in response to rainfall; and attention has been drawn to breeding and moult occurring at the same time (IMMELMANN, 1963; SERVENTY, 1971). Thus the lack of rhythmicity has been emphasised, and has been interpreted as an adaptation to lack of regular seasonal rain and no predictable seasonal abundances of food.

During a five-year field study of Budgerigars I looked at lipid deposition, moult, movements and breeding. Data on lipids and moult came from field sites in inland mid-eastern Australia (Figure 1); data on movements and breeding came from these sites, a questionnaire programme that covered eastern Australia, and literature records from the whole continent. Rhythmic aspects of these findings are summarized below; details are given in WYNDHAM (1978).

Background

Budgerigars range throughout the interior of Australia and at places, in particular in the mid-south and north-west, their range extends to the coast (WYNDHAM, 1978). Much of their range is arid zone, as defined by GIBBS (1969), but they also extend into better watered regions, in particular in the north and south. Breeding records suggest they breed throughout their range (WYNDHAM, 1978).

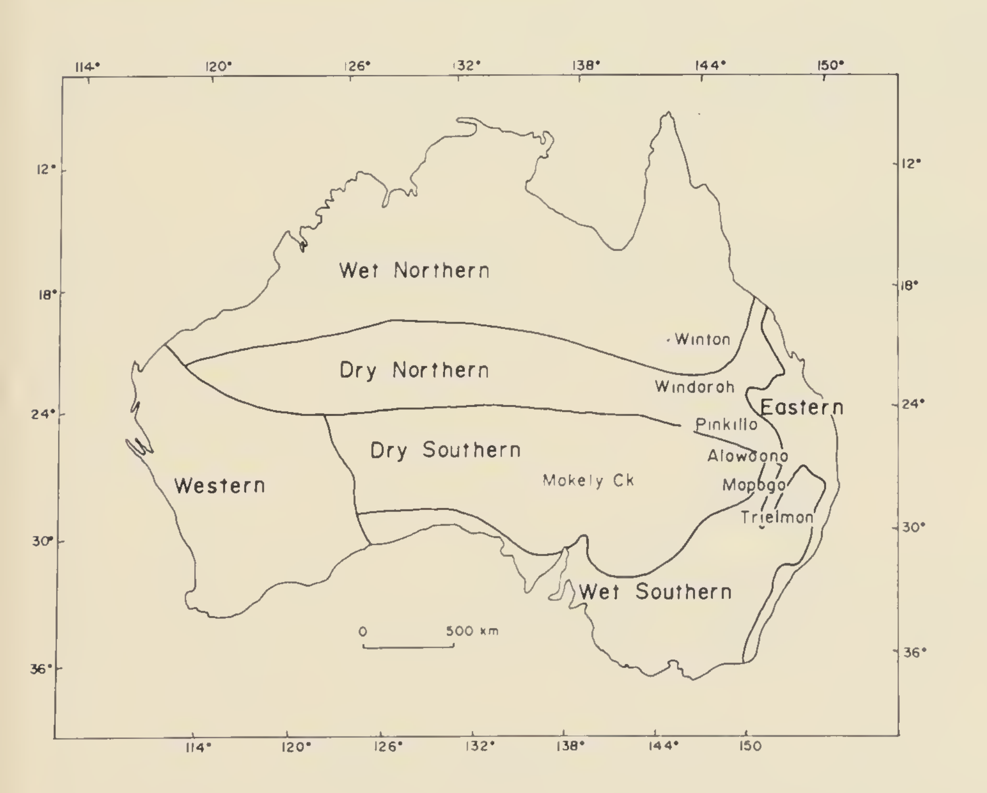


FIGURE 1. Continental Australia divided into bioclimatic zones, showing sites at which field studies were conducted.

School of Australian Environmental Studies, Griffith Univ., Nathan, Australia 4111.

In Figure 1, Australia is divided into bioclimatic zones (sensu NIX & AUSTIN, 1973); characteristics of each zone are summarized in Table 1. These zones were developed from models of climatic patterns and pasture growth developed by FITZPATRICK & NIX (1970), NIX & AUSTIN (1973) and NIX (1976); in the interior the importance of microtopography (see DAVIES, 1968, 1975, 1976 a, b,; MOTT, 1972, 1973, 1974) is taken into account. It is assumed that there are sharp boundaries between zones; in fact, there are gradual transitions from one zone to the next.

The Budgerigar's food consists entirely of seeds of ground plants, principally of grasses (Gramineae) and chenopods (Chenopodiaceae). There are no special dietary requirements during breeding.

TABLE 1: A classification of the Australian environment into bioclimatic zones. (Eastern and Western zones are excluded; these are largely outside the range of Budgerigars.)

Zone	Characteristics
Wet northern	Regular growth of pastures in summer and autumn in response to monsoonal rains. No growth in winter and spring due to lack of soil moisture except at sites of unseasonal winter rain. Temperatures favourable to growth throughout year. For birds, during a year heat stress exceeds cold stress.
Dry northern	Dominance of growth in summer and autumn in response to monsoonal rains; some growth in winter and spring in response to winter rains. Due to variable rainfall growth response varies between years, but in most years there is seed production in run-on areas. Temperatures favourable to growth throughout year. Heat and cold stress of about the same magnitude.
Dry southern	Dominance of growth in spring in response to winter rain; some growth in summer and autumn in response to monsoonal rain; little growth in winter due to low temperatures. Growth response varies between years but in most years there is seed production in run-on areas in spring, summer or autumn. Cold stress exceeds heat stress.
Wet southern	Regular growth in spring and early summer in response to winter rain; a little irregular growth in late summer and autumn at sites of aseasonal rain; no growth in winter due to low temperatures. Cold stress greatly exceeds heat stress.

Biorhythms

In adult Budgerigars, lipids averaged about 4% live weight or 12% dry weight. Birds maintained relatively constant lipid deposits throughout the year and there was no evidence of an annual cycle of deposition and mobilisation; in particular there was no build-up before movements.

Similarly, there was no evidence of an annual cycle of moult. Moult occurred during the breeding season and there was no increase in intensity of moult following breeding. In an individual a complete cycle of moult took six to eight months. A second cycle often started

before completion of the first, thus there was less than twelve months between cycles. In both sexes, birds with active gonads were often moulting.

The broad pattern of movements and breeding in eastern Australia, as emerged from the questionnaire programme, was as follows. In the south of the wet southern zone Budgerigars usually arrived in September, bred, and departed again in late December and early January. At other times of the year transients were occasionally seen but Budgerigars did not reside for long. In the mid-east of the wet southern zone, residence was not as regular as in the south of the wet southern zone. Sometimes Budgerigars were resident and bred between October and December, at other times between January and April, and at yet other times from October to May. Birds were usually absent during cold months and, if present, did not breed. In the east of the transition from the dry southern to the dry northern zone, residence most often occurred between February and April, sometimes between October and December. Breeding occurred in the hot months, mostly between February and May. In the wet northern zone, Budgerigars resided for extended periods. At times they were absent from specific sites, but there was no distinct seasonal pattern of presence and absence. In the mid-east of the wet northern zone, however, there was a tendency for reduced numbers or absence in the latter half of the year. In the north, breeding most commonly occurred in the cold months.

Historical records from the western half of the continent suggest that similar north-south trends in movements and breeding also occur in the west, but this requires confirmation.

Gonadal cycles

In non-breeding males the testes were small, the total weight averaging 0.008 ± 0.007 g (n=26). During breeding both testes enlarged greatly; the maximum total weight recorded was 0.61 g. In non-breeding females ovaries contained undeveloped follicles of average diameter of 0.80 ± 0.2 mm (n = 168). During oogenesis these enlarged to a maximum diameter of about 9 mm before ovulation. Oviducts in non-breeding birds averaged 0.006 ± 0.005 (n = 25); in breeding birds the largest oviduct sampled weighed 1.59 g.

Gonadal cycles at Trielmon are shown in Figure 2. In 1973 males arrived in early February with partially enlarged testes. Further enlargement occurred during February, then testes regressed during March and by April, before birds departed, testes had returned to a non-breeding state. In 1972, as in 1973, testes regressed greatly during the latter stages of breeding. There were also distinct cycles of gonadal activity in females. In 1973, on arrival, females had slightly enlarged oocytes and small oviducts; in April, after ovulation, ovaries contained undeveloped follicles and oviducts regressed to a non-breeding condition. Similarly, in 1972 oogenesis ceased after breeding.

At Mokely Creek, Budgerigars bred (laid eggs) from November 1973 to March 1974, and started breeding again in September. By the end of April the gonads were in a non-breeding condition. In June there was partial recrudescence of testes and slight enlargement of follicles, but by mid-July the gonads had again regressed to a non-breeding state. In May and July no breeding behaviour was seen, but in June birds courted and inspected nest-holes. I inspected nest-holes in June and July but found no nests; also there were no juveniles present in October.

Studies of caged birds have failed to reveal testicular cycles (BROCKWAY, 1964 a; VAN TIENHOVEN et al., 1966), and BROCKWAY (1964 a) proposes that in the field males maintain enlarged testes so they can breed quickly when the environment becomes favourable. My findings showed distinct gonadal cycles in both sexes and in non-breeding birds gonads become inactive. In the field, in non-breeding birds, testes were smaller than the minimal

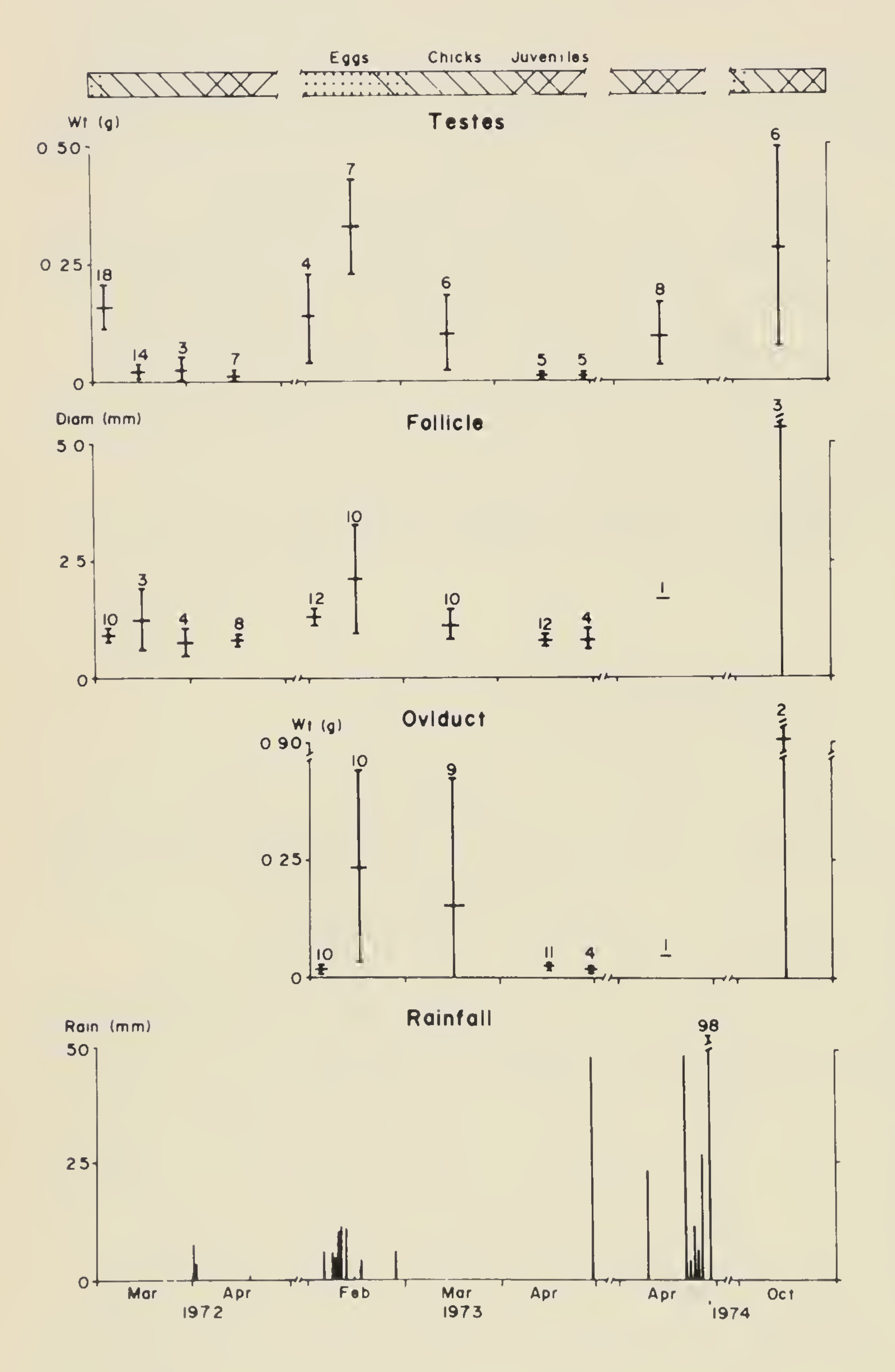


FIGURE 2. Reproductive cycles of adults at Trielmon, showing total weight of testes, diameter of largest follicle, weight of oviduct, and daily rainfall recorded 1 km from site. Mean, 95% confidence limit for mean and sample size are given. Also shown is the breeding cycle of the population.

sizes in caged birds reported by FICKEN et al. (1960) and BROCKWAY (1964 b); thus it appears that caged birds retain some testicular activity at all times. In caged females that are isolated from male vocalisations ovarian follicles regress to slightly less than 1.0 mm diameter (BROCKWAY, 1964 b). This is comparable to follicles of non-breeding females in the field.

Control of rhythms

Currently it is believed that in birds annual cyclic events (lipid balance, moult, movements and breeding) are linked and coordinated in a core control system (FARNER, 1967; WEISE, 1974). External information acts on this control system so that cyclic events occur at a suitable time, e.g. when food is abundant and/or the climate benign. Below I discuss external information that in Budgerigars may control the timing of movements and breeding.

A proposed system of control should explain the following facts. Budgerigars breed in cages and caged males retain some enlargement of testes at all times. In the field Budgerigars have distinct gonadal cycles and, when not breeding, gonads regress greatly. In the far south of the continent movements are strongly seasonal, but in mid-latitudes and in the north birds may display seasonal movements or be resident for long periods. In the far south breeding is strongly seasonal and occurs in spring; in mid-latitudes breeding may occur in spring, summer or autumn but not in winter; and in the north breeding mostly occurs in winter.

Photoperiod

This is generally thought to be unimportant as external information in Australian arid zone birds, as good seasons, movements and breeding occur irregularly (FARNER, 1967; IMMELMANN, 1971; SERVENTY, 1971; WEISE, 1974). In the Budgerigar, at places there is some regularity in movements and breeding, thus photoperiodic control may be involved. Experiments suggest that there is no photoperiodic control of spermatogenic cycles (VAUGIEN, 1952, 1953; MARSHALL & SERVENTY, 1958; POHL-APEL & SOSSINKA, 1975); however, short days (less than 12 h light) may inhibit laying by females (PUTMAN & HINDE, 1973; SHELLSWELL et al., 1975; GOSNEY & HINDE, 1976).

During winter in the southern parts of their range Budgerigars experience short day-lengths: at 35° S the shortest day is 9 h 48 min. These short days may inhibit laying by females. In the north the shortening of days is not as great (at 20° S the shortest day is 10 h 55 min) so photoperiodic inhibition of laying may not occur to the same extent.

While partial photoperiodic control of annual rhythms is thus feasible, the flexibility and variability in timing of breeding and movements in mid-latitudes suggests other factors are also involved.

Rainfall and water

Rainfall and/or its effects are commonly thought to be important in control of breeding in Australian arid zone birds (FARNER, 1967; IMMELMANN, 1971; SERVENTY, 1971; WEISE, 1974). IMMELMANN (1963) reports that a pair of Budgerigars started courting shortly after a heavy fall of rain.

For rain to act as a suitable stimulus to breeding it must precede a period of abundant food. This will occur when temperatures are favourable and the rain is sufficient to cause seeding in perennials, and germination and seeding in annuals. However, after such rain for between one and two months food is relatively scarce, as seeds in the soil are germinating and a new crop has not set. On occasions when the rain is not sufficient for production of a

new crop of seeds, or when temperatures inhibit plant growth, the rain will not precede a period of abundance of food. In the south during cold months rainfall builds up soil moisture and later, as the soil warms up, plants respond. Budgerigars could arrive in the south at a time when it was suitable for breeding but not receive a stimulus from falling rain.

Rain fell in the month before and/or during laying at Trielmon in February 1972 and 1973 (Figure 2) and at Mokely Creek in November 1973, February and October 1974. However, at Trielmon in 1973 there was good rain during April yet the birds left the area. Again, at Mokely Creek in 1974 there was good rain in April and May; gonads developed in June but no birds bred.

There are no reports that rainfall is a breeding requirement for caged birds. The fact that this has not been reported, despite extensive breeding in cages, is evidence against rain being important.

Thus it is unlikely that falling rain alone controls breeding. FARNER & SERVENTY (1960) and FARNER (1967) propose that in the Zebra Finch *Poephila guttata* testes are maintained in an active state unless inhibited by a shortage of drinking water. Over much of eastern inland Australia there are numerous man-made permanent and semi-permanent waters in tanks, dams and bore drains, thus at all times, except for extreme droughts, there are many sites with ample drinking water. On two occasions I found Budgerigars with testes of minimal size when there was ample drinking water in bore drains. At Trielmon in 1972 and 1973 testes regressed from an active state while water remained constantly present in a ground tank; at Mikely Creek testes cycled while water remained constantly present in a creek. Thus, availability of drinking water does not appear responsible for the cycles observed during this study.

Temperature

SERVENTY & MARSHALL (1957) propose that rain provides the initial stimulus for breeding, but breeding is inhibited by low temperatures. This explains adequately the partial recrudescence of gonads, but the failure of breeding to occur, at Mokely Creek in June 1974. It is thus possible that there is a threshold temperature below which breeding does not occur. In the south of the continent temperatures may drop below this threshold in cold months but in the north remain above it all the year.

Food and Nutrition

JONES & WARD (1976) show that in the Quelea *Quelea quelea* breeding is closely linked to protein and lipid balances. They propose that breeding occurs when there are sufficient protein reserves, and terminates when reserves become depleted. In the Budgerigar, annual cyclic events may be controlled by their nutritional balance. This will depend on the supply of seeds, the time available to forage, and energy demands of the body.

When an abundance of food occurs it may be of extended duration. Seeds first become available on plants and then, after being shed, remain available in the soil. As the phenology of plants differs, there may be sequential peaks of abundance, and as one species becomes scarce Budgerigars may switch to another that is becoming abundant. When a good crop of seed occurs, it should last sufficiently long for birds to commence breeding as food becomes plentiful and fledge their young before the abundance declines.

The broad pattern of movements and breeding fits with the seasonal nutritional balance for each bioclimatic zone, as predicted from the information in Table 1. In the north, growth in summer and autumn produces abundant seed in autumn and winter, but unless there is unseasonal rain, shortages may occur in late spring and early summer. During winter the energy demands of thermoregulation are low. In the far south, growth in spring produces abundant seed in late spring and early summer. Throughout the south of the continent in winter days are short and temperatures are low, thus plant growth is inhibited and the energy demands of thermoregulation are high.

Caged birds are usually kept in mild temperatures and supplied with food ad libitum; this may account for their maintaining some testicular enlargement at all times.

In conclusion, no definite statements can be made on what external information is used by the core control system of Budgerigars. Control by rainfall or availability of drinking water does not satisfactorily explain my field observations; also, from theroretical considerations, rainfall is unlikely to be a dominant factor in control. Photoperiod and temperature may act on the control system directly; alternatively they may affect the food supply and nutritional balance. The relationship between nutritional balance and breeding needs further investigation.

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Reproductive Strategies of Estrildid Finches in Different Climate Zones of the Tropics: Gonadal Maturation

Roland Sossinka

Breeding periodicity in birds is ultimately controlled by those environmental factors, or combination of factors, which affect the survival of the offspring. The time-span for successful breeding can be very short or long, and can recur periodically or sporadically, according to the climate and related ecological conditions of the area to which the population is adapted (for review, see Immelmann, 1971). Outside the breeding period, the gonads of the birds are in a quiescent state for energy-conservation.

The process of gonadal recrudescence and activation of those parts of the organisms, which take part in reproduction directly or indirectly, is governed by the hypothalamus-hypophyseal axis, which controls the release of gonadotropins. The gonadotropins induce gonadal growth, maturation of germ cells and production of sexual hormones. Sexual (and partly gonadotropic) hormones are directly or indirectly responsible for phenomena such as bill and feather pigmentation, moult, and the appearance of sexual behaviour patterns.

This process of sexual maturation is the same in adult birds with quiescent gonads after a non-breeding period and in young birds with quiescent gonads before their first breeding period. With very few exceptions, all passerine birds attempt to breed in their first year of life. The exact time when they initially reproduce differs from species to species and ranges from 10 to as much as 40 weeks of age. One would expect natural selection to result in precocity, because those genes which promote the fastest rate of reproduction will tend to accumulate in the gene pool. This tendency may be limited by other processes that require a large amount energy, such as growth of bones, muscles, or feathers in the young. If sexual maturation is too show, on the other hand, there is a risk of missing the season when the ultimate factors are present.

In order to investigate possible differences in the temporal pattern of sexual maturation, we analyzed the maturation of primary and secondary sex characters in young males of different species of the family Estrildidae. Within this well defined family, the development of the nestlings and the growth of the fledglings are rather uniform (Sossinka, 1978). So, differences in the age of puberty should be due to the ultimate control of breeding periods in those climate zones, from which the birds are derived, and should thereby reflect species- or population-specific adaptation to climatic conditions.

Materials and methods

All birds investigated were bred in captivity. The strains used were not or only slightly domesticated. The effect of domestication on sexual maturation was studied in detail in the Zebra Finch, the species which is thought to have been domesticated for the longest period. Only small and mostly insignificant differences could be found (Sossinka, 1970).

The birds were bred in indoor or heated outdoor aviaries, in long-day conditions (light 06.00 to 20.00, in summer time additional day light: Bielefeld 52°02′ N, 8°30′ E). The

Verhaltensphysiologie, Universität Bielefeld, Postfach 8640, 4800 Bielefeld 1, Bundesrepublik Deutschland.

young were removed from their parents at about 35 days of age and kept in heterosexual groups in cages on the same light regime as above, at 21–24° C and 50–75% humidity. They were fed a diet of mixed seeds and millets, sprouted millets, multi-vitamin emulsion in the water and additional food (beetle-larva, egg-food) as much as necessary. At regular intervals body measurements and moult were recorded, and the gonadal size was measured by laparotomy. The volume was calculated from the length and the width of the left testis as measured with a surgical microscope, and is expressed as the logarithm base 10 of the $mm^3 . 10^{-2}$, with error around ± 2%. Repeated laparotomy produced no noticeable effect on sexual maturation, as comparison with control birds showed.

Three different types of climate zones of the Tropics were chosen, and some of the Estrildid species of each zone were investigated. Type A comprises areas with only slight seasonal changes, for example the edge of the tropical forest, bordering the savannah. Type B comprises areas with pronounced seasonal changes, near or even outside the tropic, with monsoon or mediterranean climate. Type C comprises semi-arid to arid areas, characterisized by erratic rainfall. For each type, species from different parts of the world were investigated, belonging to either the Ethiopian, Oriental, or Australian-Papuan Region. The species investigated and their distribution are as follows.

Climate type A

1. *Lagonosticta senegala* (Fire Finch): Most parts of Mid-Africa (believed to live in the ancestral habitat of the family).
2. *Lonchura* (= *Lepidopygia*) *nana* (Madagascar Mannikin): Madagascar.
3. *Erythrura psittacea* (Red-headed Parrot Finch): New Caledonia.

Climate type B

4. *Lonchura p. punctulata* (Indian Spice Finch): India.
5. *Emblema guttata* (Diamond Firetail): Southeastern Australia

Climate type C

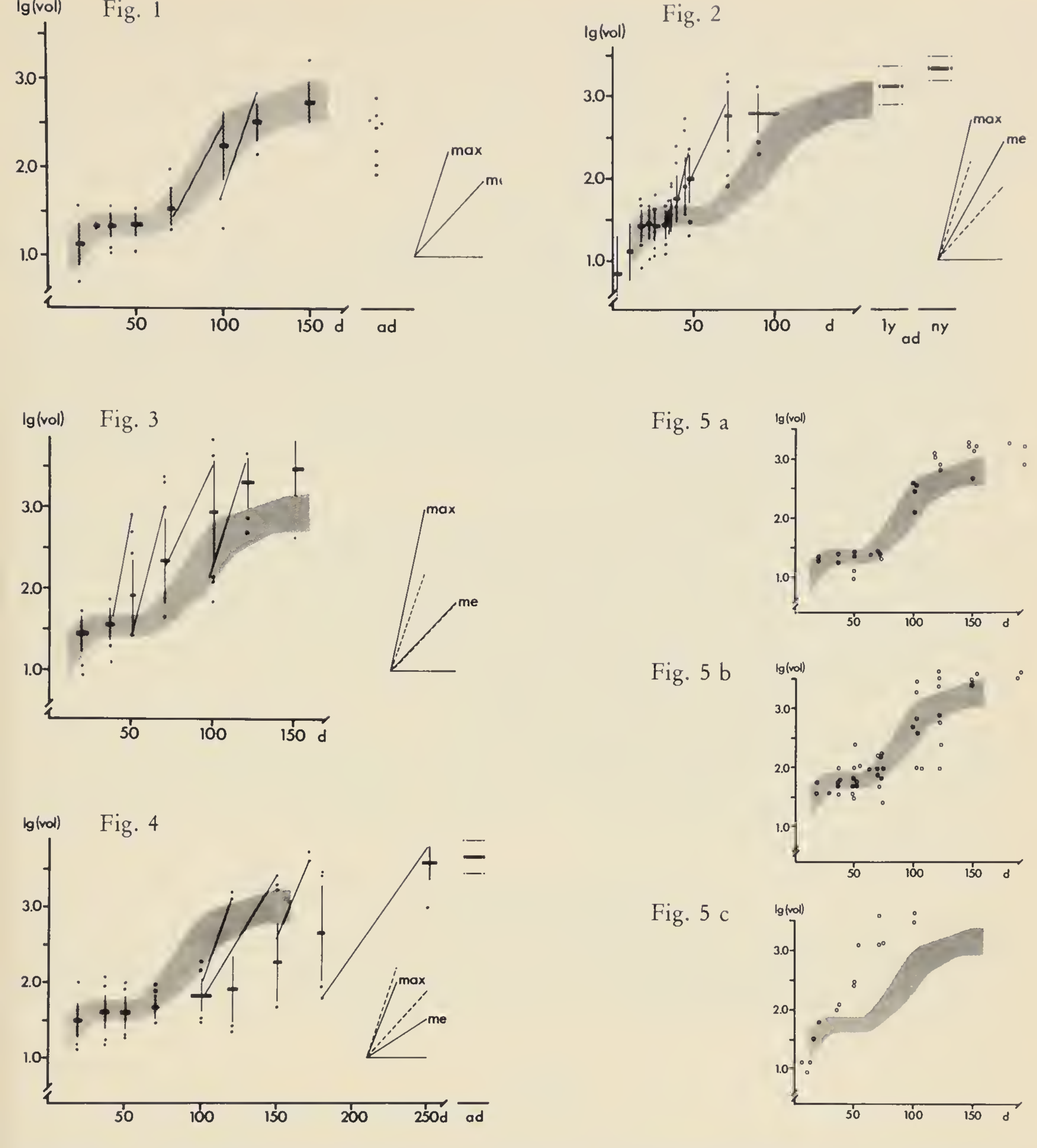
6. *Poephila g. castanotis* (Zebra Finch): Nearly all parts of Australia, especially the interior.
7. *Amadina erythrocephala* (Red-headed Finch): Interior of southern Africa.

(In some of the species (2, 5, 7), only preliminary data from a small number of birds are available.)

Results

In all species investigated, growth of the young and sexual maturation are of the same general pattern, but there are pronounced temporal differences in the age when sexual maturity is attained. Body growth and the moult of the juvenile coloured feathers are complete at 25 to 30 days of age and independence is attained at 30 to 35 days of age.

Testicular growth ceases in all species around the age of fledging (18–21 days). The gonads then rest in a state comparable to that of the quiescent gonads of adult songbirds outside the breeding period. Histological examination indicates stage 2 to 3 (according to BLANCHARD, 1941) which is the same as in photo-sensitive birds during the refractory



FIGURES 1–5. Relationship between testis volume and age in seven Estrildid finches. 1, *Lagonosticta senegala:* sample sizes 11, 3, 18, 13, 10, 11, 9, 7, 8. 2, *Erythrura psittacea:* sample sizes 16, 12, 16, 16, 18, 12, 9. 3, *Lonchura p. punctulata:* sample sizes 10, 36, 17, 13, 34, 28, 22, 12, 15, 7. 4, *Poephila g. castanotis:* sample sizes 8, 9, 23, 12, 24, 13, 10, 14, 21, 28, 22, 37, 16, 16, 13. 5 a, *Lonchura (= Lepidopygia) nana.* 5 b, *Emblema guttata.* 5 c, *Amadina erythrocephala.*

Conventions: broad bars crossed by vertical lines = mean per sample ± standard deviation; single dots = maxima or minima per sample; grey area = means with standard deviation in *Lagonosticta senegala* for comparison; shifted along ordinate in proportion to body weight; open circles = preliminary data points; d = age in days; ad = adult; 1y = one year; ny = several years; me = medium slope; max = maximal slope; dotted line = slope in *Lagonosticta senegala* for comparison.

period (Marshall, 1952). The onset of subsequent gonadal growth, however, is very different among the species of the different climate types, and the rate of development, as indicated by the slope of the logarithmic growth, also differs. The growth-curves of testis volume, which are very well correlated with the stages of spermatogenesis (see Sossinka, 1974), are shown in Figures 1 to 5 in detail.

Three different temporal patterns can be discerned:

1. A fairly rapid rate of maturation, leading to sexual maturity at around 4 months of age, after a period of growth starting at less than two months. This is typical for *Lagonosticta senegala, Erythrura psittacea* and *Lonchura nana,* which are all from climate type A. There is some inter-individual variation in testis growth (most pronounced in *Erythrura psittacea*), which makes the mean slope less steep than the slopes for individual birds. (Data from birds with no change in volume because they have not begun development or have already reached adult size are combined with data from birds with gonads actually undergoing development.)
2. A slow rate of maturation with recommencement of gonadal development starting after $2^1/_2$ months of age and in some birds not before 4 or 5 months. Most birds attain sexual maturity at 6 to 9 months of age, although a few individuals mature at 4 to 5 months. There is pronounced individual variability. The mean as well as the maximal slope is smaller than in pattern 1. Examples: *Lonchura p. punctulata,* and – at least in its tendency – *Emblema guttata;* both climate type B.
3. An extremely rapid rate of maturation, with only a short period of quiescence. Sexual maturity is attained at 2 to $2^1/_2$ months of age. Small individual variability. The mean slope is much steeper than in pattern 1. Examples: *Poephila g. castanotis* and *Amadina erythrocephala;* both climate type C.

The moult into the adult-coloured body feathers starts in all species shortly before the recommencement of gonadal development and in general is nearly finished before the end of testis growth. Usually, there is a short phase of very heavy moult, which in birds of pattern 3 coincides with gonadal increase, whereas in birds of pattern 2 these processes exclude one another.

Discussion

Pronounced differences in the temporal patterns of sexual maturation have evolved in the more or less closely related species investigated. As species living in the same type of climate exhibit similar patterns, the patterning is due primarily to the climate-dependent ultimate control of the breeding period. The fairly rapid rate of maturation (pattern 1) occurs in areas where breeding is restricted for only short periods in the course of the year. Gonadal growth is not as rapid as in pattern 3, because there is no special selection pressure towards precocity and there is another growth-process requiring energy: the moult from the cryptically coloured juvenile plumage to the releaser-emitting adult plumage (which is necessary for successful pair-bonding – compare Nicolai, 1968 – and therefore should take place before maturity). The extremely rapid rate of maturation (pattern 3) in arid areas with erratic rain, which subjects the birds to the energetic load of simultaneous moult and gonadal growth, is caused by the irregularity of the rainfall which is responsible for the appearance of the ultimate factors. All males, including young of the year, have to be pre-

pared to begin breeding at any time of the year, and young males should attempt to breed as early as possible, even in the same vegetation-period in which they were hatched (see IMMELMANN, 1962; SERVENTY, 1971; SOSSINKA, 1974). This risk of energetic overload can be avoided with a slow rate of maturation (pattern 2) in climate zones where because of regular and pronounced seasonal changes the next breeding will not take place until 9 months later. Moult and gonadal growth proceed slowly and alternately.

The very high individual variability in the annually breeding species with pattern 2 indicates the lack of some external synchronizing factor under constant laboratory conditions. In India, gonadal development in free-living *Lonchura p. punctulata* is very uniform (THAPLIYAL & PHANDHA, 1965). In the species with pattern 3, the start of gonadal maturation is exclusively internally programmed. In these opportunistic breeders no external factor can be used as a proximate factor to predict the irregular occurrence of ultimate factors. Similarly, a strong endogenous factor is responsible for gonadal growth in the species breeding throughout most of the year according to pattern 1. But, as the moderate amount of variability in *Lagonosticta senegala* indicates, some additional external factors may be acting. In Africa, climatic and dietary factors can retard maturation and thereby prevent those young from becoming sexually mature (and breeding in the unfavourable season), which were born some time before the disappearance of the ultimate factors (MOREL, 1969). In *Erythrura psittacea* a very high variability indicates the important role for external regulation. This is probably a relict character of the grass-eating ancestors of this genus (see ZISWILER, 1972), which lived in zones with a more restricted breeding period.

In general, temporal patterning of sexual maturation is highly adaptive. Similar patterns have evolved convergently in different parts of the world, and they are probably not reliable indicators of taxonomic affinities.

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SYMPOSIUM ON PATTERNS OF BIRD MIGRATION THE GEOGRAPHICAL, METEOROLOGICAL AND CLIMATOLOGICAL ASPECTS

10. VI. 1978

CONVENERS: S. A. GAUTHREAUX AND G. ZINK

Autumn Landbird Migration over the Western Atlantic Ocean as Evident from Radar

W. John Richardson

Introduction

Most landbirds in easternmost North America migrate southwest parallel to the coast during autumn, but some move SE-SSW offshore (Drury & Nisbet, 1964; Richardson, 1972). Some of the latter change course and return NW to land (Baird & Nisbet, 1960; Murray, 1976; Richardson, in press), and others become exhausted and apparently perish at sea (Scholander, 1955). However, some are still aloft 2000 km from shore (Penard, 1926; Williams et al., 1977b), and some fly to Bermuda (Wingate, 1973) or even Europe (Sharrock, 1974). Radars on Bermuda, the West Indies and ships have recently shown that many landbirds fly non-stop from SE Canada and NE U.S.A. to the West Indies (2550–3300 km), and perhaps even South America (a further 800 km). The Blackpoll Warbler *Dendroica striata* seems to be a major user of this route (Nisbet, 1970).

I present here new data about offshore departures from Nova Scotia, Canada, and then summarize evidence concerning landbirds over the western Atlantic in fall. Spring migration and autumn shorebird migration in this area are reviewed in Richardson (1974, 1979), and southeast flights from Florida along the West Indies are described by Richardson (1976) and Williams et al. (1977a, b).

Southward departure from Nova Scotia

One or more of three surveillance radar sites in Nova Scotia and one in New Brunswick were used in 1965 and 1969–71 (Fig. 1; for methods, see Richardson, 1972, 1979, in press). The most reliable data were from Barrington, N.S., in 1971 and Sydney, N.S., in 1965, but landbird flights were always difficult to study. Available data are usually incomplete and/or qualitative because of (1) limited abilities of the radars for resolving echoes from passerines, (2) occasional equipment malfunctions, and (3) the fact that landbirds often flew in all directions between SE and WSW, but with modes SSE-S and SSW-WSW. Because of (3), I often could estimate modal directions, but could not assign all individual echoes to one or the other group, and so could not calculate the mean or dispersion of directions of the SSE-S group.

Unequivocal southward landbird departures of at least moderately high density (5 on a 0–8 ordinal scale) were recorded from Barrington as early as 29 and 31 Aug. (1971) and as late as 27 and 29 Oct. (also 1971). Relative frequencies and densities in various parts of this period are uncertain, but the 31 Aug. 1971 flight was a major migration (density 7 on the 0–8 scale), and density 5 or 6 flights were frequent from mid-Sept. to late Oct. The densest SSE-S and SW flights appeared similar in density, but dense SW flights were much more common (Richardson, 1971).

Broad-front SSE-S departures were recorded by all three Nova Scotian radars, but high densities (6 or 7) were not recorded over eastern Nova Scotia. Migrants appeared 20–30

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min after sunset over all land areas of Nova Scotia within radar range-not just from coastal areas. All of western Nova Scotia was sometimes outlined on the Barrington radar display just after these birds took off. Sometimes birds from southern New Brunswick and eastern Maine also departed SSE-S. For example, on 31 Aug. and 30 Sept. 1971, the density over western Nova Scotia declined briefly about 1–$^1/_2$ h after sunset as birds from Nova Scotia moved offshore, but then increased as others from north of the Bay of Fundy moved into range over western Nova Scotia and the Gulf of Maine. The density of southward flight over western Nova Scotia usually decreased markedly by midnight. This, together with the measured mean ground speed of 51.6 km/h (n=126 echoes on 9 nights), indicates that few landbirds initiated SSE-S trans-oceanic flights more than 150 km inland from the coast of New Brunswick or Maine. Data from the St. Margarets, N.B., radar corroborate this; it commonly detected some southbound passerines, but no major southward flights were noted.

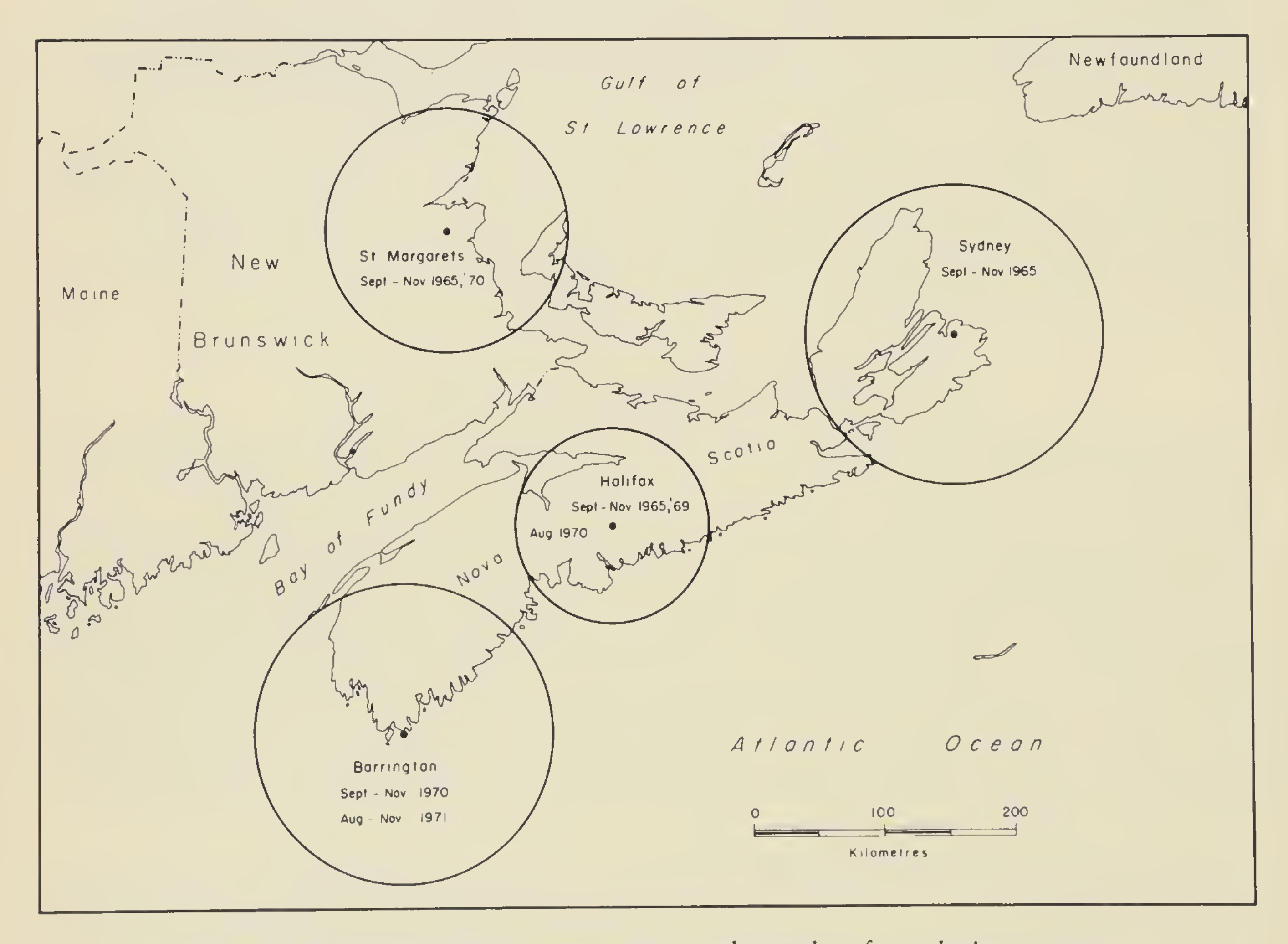


FIGURE 1. Radar locations, coverage areas and months of use during autumn.

A nodding height-finder radar at Barrington showed dense, unresolvable echoes from landbirds up to 0.6 km ASL on one evening with SSE-S but no SW landbird migration (21 Sept. 1971) and up to 1.8 km on another (31 Aug. 1971). On three evenings with both SSE-S and SW miqration (not distinguishable on the height finder) dense echoes extended up to 0.9, 1.5 and 1.8 km. In contrast, on 14 evenings with SW but no obvious SSE-S passerine migration, passerines were abundant only up to 0.6–1.2 km (mean 0.8 ± s.d. 0.2 km). These results are consistent with NISBET et al. (1963), who found that passerines

moving south from Cape Cod on 4 nights were somewhat higher (typically at 0.6–1.2 km) than other passerines.

Tracks of individual echoes were measurable at Barrington on only three evenings when there was no overlap in track distributions of SSE-S and other types of movements: 22 Sept. 1971 – vector mean 170° ± angular deviation 11.9° (29 echoes measured); 24 Sept. 1971 – 167 ± 10.5°, n=49; 30 Sept. 1971 – 171 ± 15.8°, n=66. On other nights modal tracks of the SSE-S group around 1 h after sunset ranged from ~155° (8 Oct. 1971) to ~175° (25 Sept. 1971). Some birds moved S-SSW on most of these nights, and on at least one night at Sydney the mean track of passerines just after take off was intermediate between 'typical' SSE-S and SW-WSW departures: 19 Oct. 1965 – 203 ± 11.4° (n = 41). Directional data for the SSE-S departures of landbirds were too meagre and imprecise to warrant detailed analysis, but there was no evidence of a correlation between wind direction and nightly modal direction at Barrington, and little evidence of such a correlation for all Nova Scotian sites (Fig. 2). DRURY & NISBET (1964) also found no such correlation near Cape Cod, but my data do not support their conclusion that there are two distinct directional classes (~171° and ~186°) among landbirds moving offshore.

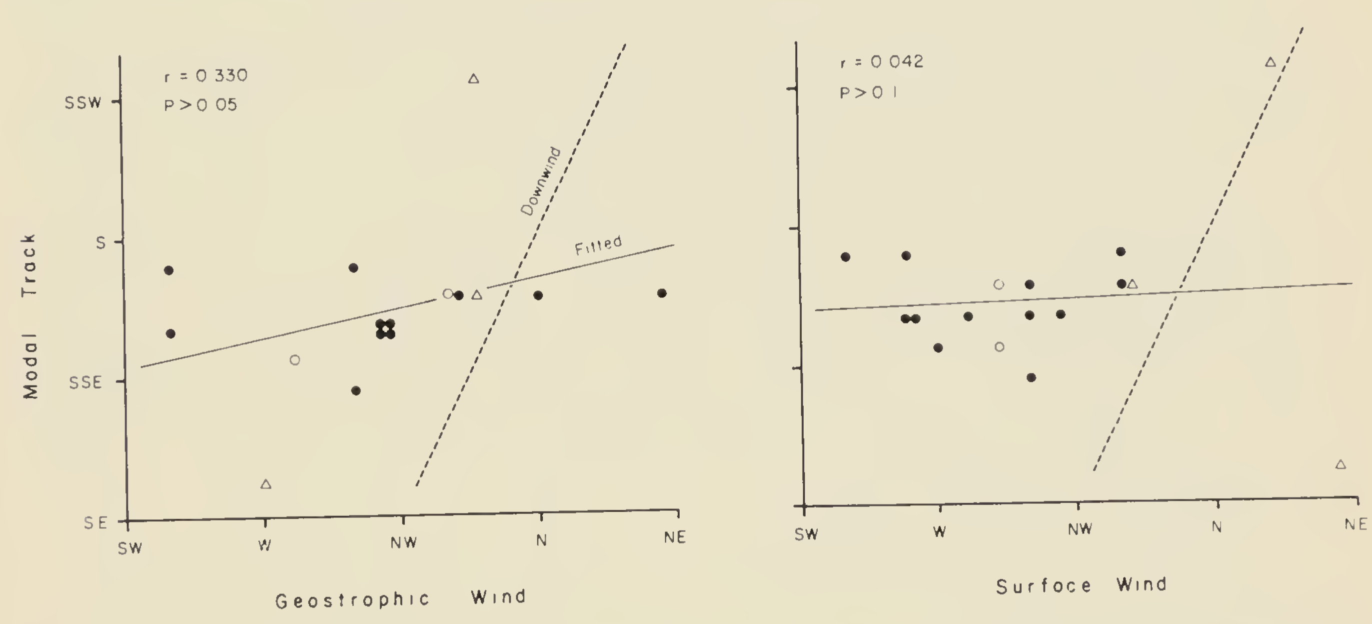


FIGURE 2. Modal track directions of landbirds departing seaward from Nova Scotia on various evenings vs wind direction. Tracks were measured about 1 h after sunset with the Barrington ●, Halifax ○ and Sydney Δ radars. One-sided probabilities are given.

On at least two evenings at Barrington the modal track shifted from 165 or 170° soon after take off to 195–205° around midnight (21 and 30 Sept. 1971). Whether individual echoes changed course is uncertain, since individuals couldn't be followed for more than ~30 minutes. On 21 Sept. the change in tracks coincided with clearing skies and a shift in surface wind from 280° at 13 km/h to 340° at 18 km/h; on 30 Sept. the wind was 300–310° at 16 km/h and the sky was at least partly clear all evening. These were also the only two occasions when an evening departure to the SSE-S was followed by a pre-dawn reorientation of birds over the sea from SW to NW.[1] It is unlikely that any of the individuals that departed SSE-S in the evening were moving SW within radar range of the

[1] Evening departures to the SW were often followed by such reorientation (RICHARDSON, in press).

coast late in the night. Thus there was no proof that landbirds departing SSE-S over the ocean ever turned back to land, and considerable evidence that few if any did so.

Most offshore departures occurred with west, northwest or north winds. Of 26 definite cases of density 4–7 SE-SSW landbirds departure from Nova Scotia. 4 were in WSW-NW winds close behind cold fronts, 1 was in a NW airflow SW of a low pressure area, 14 were in N, NW or N airflows north, east or near the centre of high pressure areas, 1 was in the NE airflow SE of a high, 2 were in the SW airflow NW of a high, and 4 were in unclassifiable circumstances having W, NW or N winds. Offshore departures of landbirds were more frequent with NW than NE winds, whereas SE departures parallel to the coast were more frequent with NE winds (Richardson, 1972, 1978). Thus offshore departures tended to begin sooner after cold front passage than peak SW departures. The 21 Sept. 1971 departure (see above) began under overcast during cold front passage.

Landbirds over the Atlantic

The Blackpoll Warbler is the only landbird whose main fall route has been shown to be from NE U.S.A. and SE Canada over the Atlantic to the West Indies and South America (Nisbet, 1970; Ralph, 1975). However, Blackpolls – like other species – sometimes return NW to land after dawn (Murray, 1965), and late Aug., early Sept. and late Oct. departures evident on radar must be other species (Nisbet et al., 1963). Few North American passerines reach the West Indies before mid-Sept. (McCandless, 1962; Richardson, 1976), so birds moving offshore earlier may be poor orienters that will perish at sea (Ralph, 1975). Other warbler species seen south of Bermuda (Penard, 1926; Williams & Williams, in press) and major SSE-SSW arrivals of landbirds at Puerto Rico in late Oct. (Richardson, 1976) may leave the coast south of New England, but specific evidence about their take-off locations is lacking. Offshore departures occur at least from eastern Nova Scotia to New Jersey (Drury & Keith, 1962; Swinebroad, 1964; this study), and probably to Virginia, where birds with low airspeeds depart east of 170° (Williams et al., 1977b).

Landbirds tend to depart SSE-S with cool W, NW or N winds behind a cold front or in the eastern or central parts of a high pressure area (Drury & Nisbet, 1964; Richardson, 1972, this study; Williams et al., 1977b). Fronts often stall before reaching Bermuda. Some landbirds[2] that catch up with such fronts penetrate them and continue SE-SSW in the typically fair weather of the 'Bermuda High', but others apparently fail to penetrate to the High and may perish (Williams & Williams, in press). Species differences and factors affecting the probability of penetration are unstudied.

Few Blackpoll Warblers land at Bermuda (Nisbet et al., 1963; Ralph, 1975), and radar shows passerines and other birds passing overhead, usually SE (Ireland & Williams, 1974). Peak daytime passage (all species) is in the afternoon, ~18–22h after evening departure from coastal areas 1100–1550 km away (Williams et al., in press). However, nocturnal radar data from Bermuda are meagre, and many passerines may arrive at night >24 h after take-off (Nisbet et al., 1963). Ship radars show that SE-SSW migration, probably of landbirds[2], can extend 1000 km east and 800 km south of Bermuda (Williams et al., 1977b).

[2] My assumption, based on the low altitudes (the radars used couldn't detect birds above 500–1000 m), generally low airspeeds, and visual sightings reported by Williams & Williams (in press).

Radars at Puerto Rico and Antigua, West Indies (~1650 km S of Bermuda), often show birds approaching from the NW, N and even NE (HILDITCH et al., 1973; RICHARDSON, 1976; WILLIAMS et al., 1977b). Some are shorebirds, but low airspeeds at both sites, plus echo characteristics and abundance at Puerto Rico, indicate that many – including some at 4–6 km ASL – are passerines. Some (passerines?) pass Puerto Rico and most pass Antigua without stopping, apparently continuing ~800 km to South America. Imprecise relationships between times of known or suspected departure from NE U.S.A./SE Canada and arrival in the West Indies suggest a mean transit time (all species) of 60–70 h to the northern West Indies and 82–88 h to South America (RICHARDSON, 1976; WILLIAMS et al., in press).

NISBET et al. (1963) concluded that Blackpoll Warblers, based on weights at departure from New England and arrival at Bermuda, could fly for >95 h. GREENEWALT (1975) calculated a still-air range of 3465 km for Blackpolls. However, present theory indicates that these are overestimates (TUCKER, 1975, 1976). Since from Boston it is a minimum of 2700 km to Puerto Rico and 3400 km to Venezuela, the observed tendencies to take off with following NW winds and to approach the West Indies at high altitudes, where winds are often most favourable (RICHARDSON, 1976; WILLIAMS et al., 1977b), must have high adaptive value. High altitude flight may also conserve water (BERGER & HART, 1974) and increase airspeed (PENNYCUICK, 1975). Increased airspeed would decrease transit time, and thus reduce the risk of encountering a hurricane. Strip-like updrafts behind cold fronts might be useful in conserving energy early in the flight (GRIFFIN, 1969), but there is as yet no evidence that landbirds concentrate in the rising air.

Mean tracks of the landbirds are ~170° just after take off but ~190° near Puerto Rico. WILLIAMS & WILLIAMS (in press) suggest, considering shorebirds and landbirds together, that the entire flight is made with a constant SE heading, and that lateral wind drift causes the curved route. However, early in the flight most landbirds maintain SSE-S tracks by adjusting their headings around a mean of ~S to correct for wind drift (DRURY & NISBET, 1964; this study). At Puerto Rico, tracks (all species, but mainly passerines) are strongly correlated with wind, and result from uncorrected drift by the prevailing easterly trade winds from a mean heading of 174°.[3] In mid-ocean, headings of landbirds[2] average about 163° (WILLIAMS & WILLIAMS, in press). Thus, mean track, the relationship of headings to wind, and possibly mean heading change en route. The ultimate reason for the curved route is presumably a function of prevailing winds and energy conservation, but precise orientational processes and the energetic advantage over alternate routes are uncertain, and should be further examined for landbirds alone.

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[3] Calculated assuming that the birds are at the altitude with the most favourable wind (RICHARDSON, 1976). Other calculation procedures give means of 166–174°.

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Migration Patterns of Waders (Charadrii) in Europe

A. J. PRATER

Since the pioneering study by NORREVANG (1959) there has been considerable attention paid to the study of migration of waders in Europe. During the last ten years the co-ordinated ringing and counting programmes of amateur and professional ornithologists have resulted in the publication of many detailed papers. Recently GLUTZ, BAUER & BEZZEL (1975, 1977) have provided detailed summaries of the current knowledge about wader migration in Europe. This brief review will not attempt to duplicate their work but will concentrate on general patterns of wader migration.

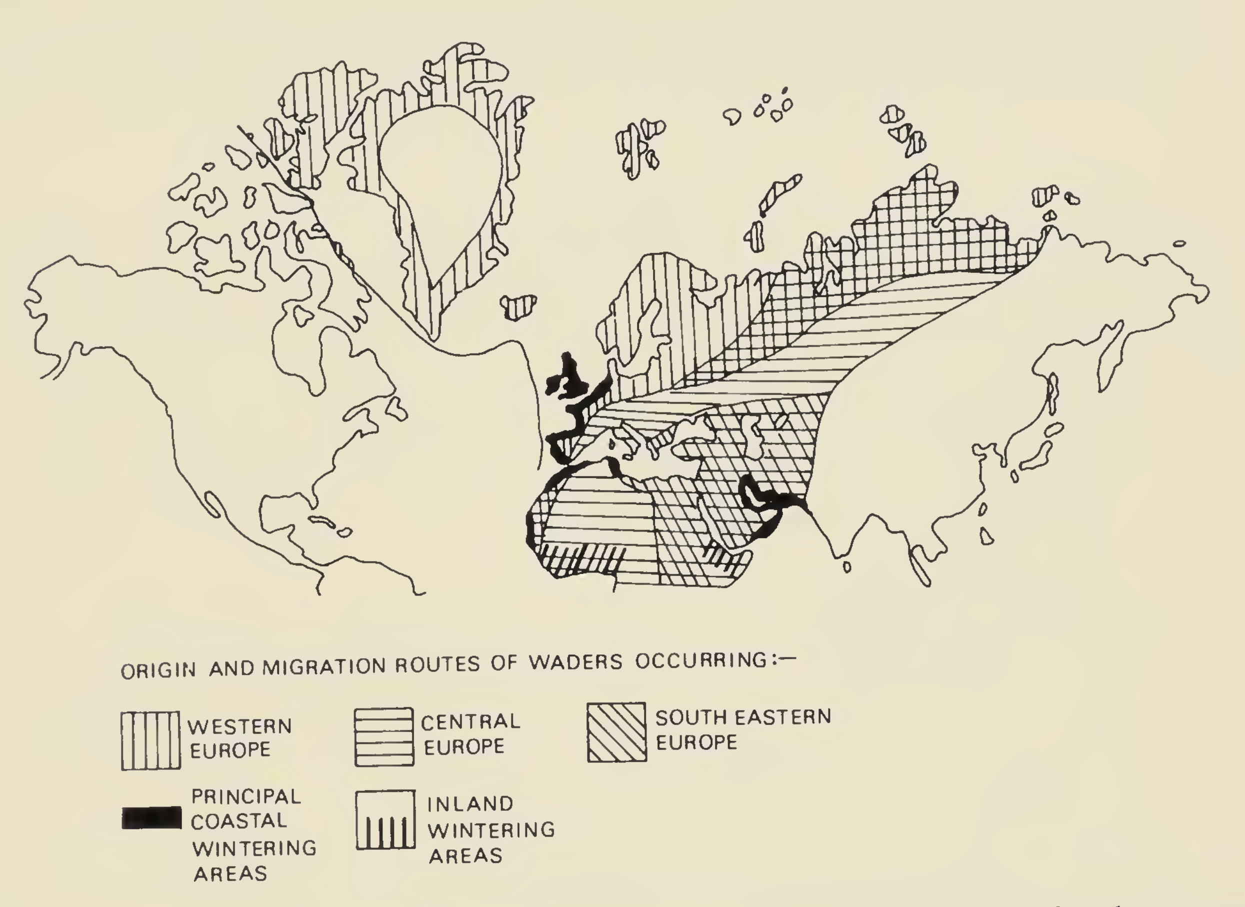


FIGURE 1. The relationship between breeding, migration and winter distributions of waders occurring in Europe.

Origins of populations

Waders, which occur in Europe on passage or during the winter, breed in a large area of the Arctic and temperate zones of the world. Figure 1 shows the known extent of this area based on ringing recoveries; it stretches between 130° (possibly 140°) E and 90° W. Unfortunately the relatively small number of migrant waders ringed in southeastern Europe have not provided enough evidence as to their origins. The boundaries, particularly in the Palaearctic, shown in Figure 1 should only be considered as a guide but they do represent the principal origins of waders seen in Europe and, by implication, the direction of movement too. It should be noted that vagrant individuals have been recorded from

British Trust for Ornithology, Beech Grove, Tring, Hertfordshire, U. K.

further south and east especially further west. However, this aspect of migration will not be considered here.

Of the species regularly occurring in western Europe those originating from the extremes of this range are the high arctic breeders. In zoogeographical and evolutionary terms, as used by LARSEN (1957) for example, these correspond to the super cold forms. Those migrating from slightly less far are basically the sub-cold forms, while the temperate and warm forms occur progressively less often in western and more frequently in south eastern Europe.

Two major divisions of wader populations can be made; they are the eastern (Palaearctic) and north western (NE Nearctic and Icelandic) breeding birds. The species involved from the Nearctic, Ellesmere and eastern Baffin Islands and Greenland, are *Calidris canutus*, *C. alba*, *C. alpina*, *Arenaria interpres* and *Charadrius hiaticula* (and possibly *Calidris maritima*). Iceland provides a similar range of species to Scandinavia and much of northern USSR but lacks *C. canutus*, *C. alba*, *Limosa lapponica*, *A. interpres* and *Pluvialis squatarola*.

The directional movements of the two divisions of populations differ. In autumn north western breeders cross the Atlantic over a wide area between northern France to southern Norway, although two principal streams go to the Irish Sea and the North Sea. The latter group occurs primarily in the Wadden Sea and many birds arrive via southern Norway and Denmark. The spring return movement is a mirror image of this, although in *C. hiaticula*, *C. alba* and *A. interpres* there is a more westerly component than in autumn. Then only a few major estuaries in the Irish Sea are utilised. Greenlandic and Canadian birds use Iceland as a major resting and feeding area during migration, apparently with a tendency for g greater use in spring.

The basic movement of Scandinavian and particularly northern Russian waders is south or southwest through the Baltic Sea and into the North Sea. There is some overland migration across southern Sweden and more obivously across Denmark. The intensity of migration appears to be slightly greater along the Swedish coast than along the southern Baltic shore. In spring there are indications that a more easterly route is taken by many of the species which breed in north and mid central USSR. This is particularly noticeable in *C. ferruginea*, *C. minuta*, *Philomachus pugnax* and *Tringa glareola*. There are, of course, many exceptions to this generalisation; the most extreme being *Phalaropus lobatus* where the north Scandinavian population moves southeast towards the Caspian Sea and the Indian Ocean.

As noted by MOREAU (1972) and for *C. canutus* by DICK et al. (1976), many long distance migrants from both Greenland and central USSR follow great circle routes. These explained the autumn occurrence of northwestern breeders in southern Norway and the extensive use of the Baltic Sea by northeastern breeders, both of which winter in large numbers on the European and north African Atlantic coasts.

Other factors influencing migration patterns

Latitude of breeding grounds

In species with a continuous breeding distribution, which spans a wide latitudinal zone, the more southerly birds move the least distance in winter. In *T. totanus* this results in the

Icelandic, Scottish and northern English breeders wintering in the same general area between 48° N and 58° N, often along with southern English birds. In this case the Scandinavian and western continental European populations move further south along the Atlantic coast. Only in a few species is leapfrog migration seen, particularly *C. hiaticula* where Greenlandic, Icelandic and northern Scandinavian birds winter south of 40° N and British, North Sea and southern Baltic breeders remain in the British Isles and France.

Age

Although it is often considered that immature waders migrate further south than adults, information on this is scarce and it is mainly of a circumstantial nature. There are fewer juvenile *C. canutus* at major British estuaries during winter than there are during the autumn passage periods. However, this decrease may also involve a change in habitat utilization. There is a tendency for juvenile British *T. totanus* and *C. hiaticula* to move further south than adults, although in *N. arquata* this is not the case.

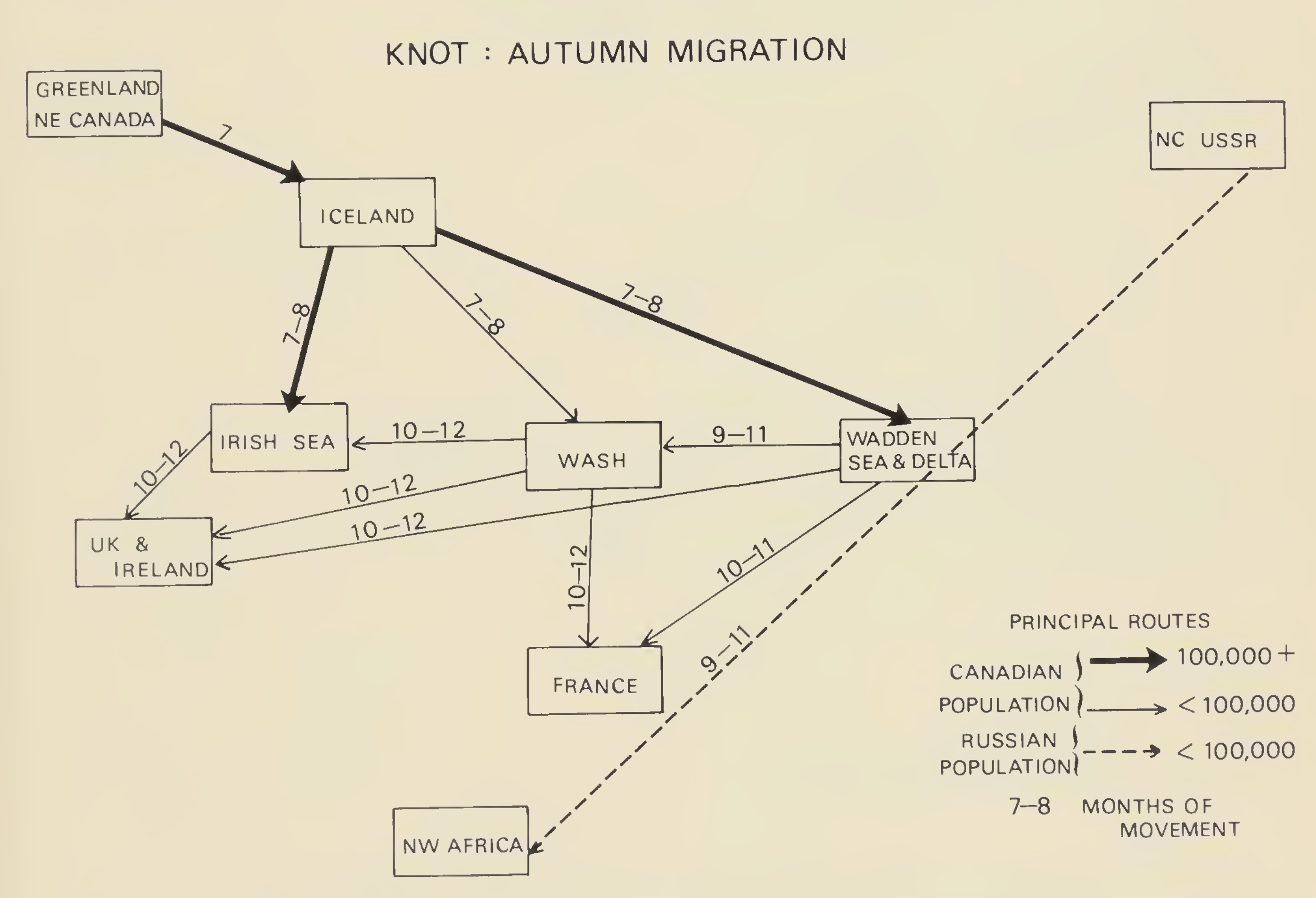


FIGURE 2. Diagrammatic representation of the autumn migration of *Calidris canutus* in Europe.

Juvenile waders, which originate from northern USSR, tend to migrate in autumn further to the west than adults. STANLEY & MINTON (1972) showed this for *C. ferruginea*, and related it to a greater tendency to be displaced from their 'normal' route by weather systems. Similarly many *C. alpina* ringed in western Norway on their first migration are subsequently retrapped as adults in the main Baltic Sea flyway. Perhaps this variability occurs among waders because there is a temporal separation in migration times between adults and juveniles; the former preceding the latter by between two and four weeks.

Sex

Data are lacking for sex ratios in different parts of the wintering range of most species. Only in *P. pugnax* has this aspect been studied; PRATER (in press) noted that females outnumber males by 9 to 1 in southern Africa, while males form the great majority of birds wintering in Europe.

Short distance movements of waders in Europe

To date little attention has been paid regular short distance movements of waders. These do not produce spectacular patterns but are of great significance in assessing the conservation importance of each estuary in the birds annual cycle. Many species of coastal waders in western Europe occur in large numbers at relatively few sites. These almost certainly move in flocks and, in view of the predictability of their occurrence, follow fairly narrow migration routes.

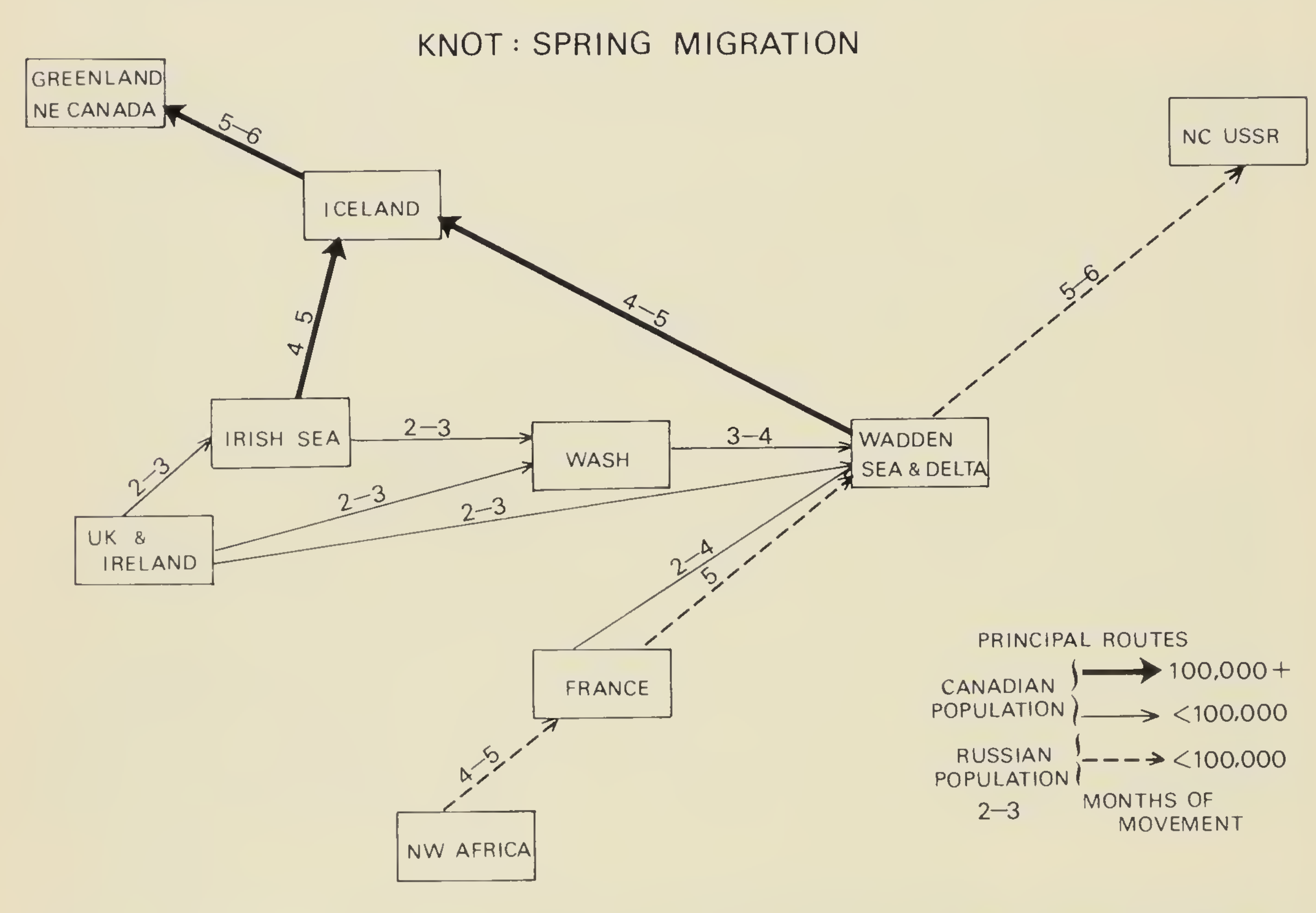


FIGURE 3. Diagrammatic representation of the spring migration of *Calidris canutus* in Europe.

The approach which integrates data from counting and ringing programmes has provided valuable information on this aspect of wader migration. Recent results for *C. canutus* illustrates this approach. The count data, Table 1, are obtained from the IWRB and are combined with ringing recovery, recapture and morphometric data to produce the diagrammatic representations of migration in Figures 2 and 3. These show clearly that there are a number of major centres for *C. canutus* in Europe. Of special value as moulting centres are the Wadden Sea, the Irish Sea and, to a lesser extent, the Wash. From here the birds move out into their wintering areas. There is a steady shift in the centre of the

population to the west and southwest at this time, resulting from a progressive displacement of birds. Subsequently they return to these same areas, in apparently similar numbers, in the spring prior to migration. The patterns of counts and of retraps and recoveries of birds ringed in the Irish Sea and the Wash indicate that these support groups of birds which are separate and stable. During autumn, spring and summer birds ringed on the Wash maintain a spatial separation from Irish Sea birds, with the former being consistently further east and in summer further north too. This occurs despite an almost complete mixing in western Britain and Ireland during the winter months. This probably also occurs in other species e.g. *C. alpina, L. lapponica.*

TABLE 1: Numbers of knot in Europe and NW-Africa, in thousands.

	late August early September	January	late August early May
Iceland	10?	0	20?
Wadden Sea + Delta	260	60	85
Wash	40	60	15
Irish Sea	120	175	110
rest of U.K. + Ireland	5	90	15
France	40	30	40?
rest of Western Europe	5?	30	5?
NW Africa	?	100	?
	480 +	545	290 +

Wader migration in Europe is a complex phenomenon involving many variables related to origins, age and sex. These are no doubt integrated with tradition, evolution and subsequent ecological adaptations. We are still a long way from being able to describe all aspects in detail but the research being carried out is beginning to allow general summaries to be made.

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Räumliche Zugmuster europäischer Singvögel

Gerhardt Zink

Zugrichtungen und Winterquartiere europäischer Vögel werden stark beeinflußt von der ungleichen Verteilung der Landflächen der alten Welt (Moreau 1952) und vom Verlauf der Küstenlinien in Europa. Die Fläche des nördlich von Afrika gelegenen Teiles Europas (bis 40° E), ohne das für viele Arten als Überwinterungsgebiet dienende Mittelmeergebiet, verhält sich zur Fläche Afrikas (ohne die Sahara, aber einschließlich der Mittelmeerländer) wie etwa 1:4, die paläarktische Region östlich von 40° E und nördlich 30° N zu den Winterquartieren in S-Asien aber wie etwa 3:1. Berücksichtigt man ferner, daß Afrika um 7 Längengrade – also etwa 700 km – weiter nach W reicht als Europa und daß die Küstenländer des Atlantischen Ozeans in Westeuropa wegen ihres gemäßigten Klimas für viele Arten als Winterquartier dienen, dann ist es nicht erstaunlich, daß südwestliche Zugrichtungen in Europa und in Westasien vorherrschen.

Zugrichtungen.

89 Singvogelarten ohne die Emberizidae, die Fringillidae und die Ploceidae, die im Atlas des Singvogelzugs (Zink 1973) noch nicht bearbeitet sind, brüten regelmäßig in oder ziehen in beträchtlicher Zahl durch Mitteleuropa. Von 7 dieser Arten sind Zugwege und Winterquartiere nur ungenügend bekannt. Eine Aufteilung der verbleibenden 82 Arten nach den Anfangsrichtungen beim Herbstzug ergibt folgendes Bild:

14 Arten sind Standvögel oder ziehen nur in geringem Ausmaß.

33 Arten haben Anfangsrichtungen westlich von S, manche davon auch nach W oder WNW, wie z. B. Stare (*Sturnus vulgaris*) von NW-Deutschland nach England.

9 Arten ziehen von Mittel- und Westeuropa mit Anfangsrichtungen östlich von S.

9 Arten haben Anfangsrichtungen zwischen SW und SE. Beim Wasserpieper (*Anthus spinoletta*) des Alpenraums sind sogar alle Richtungen von N über W bis SE möglich.

3 Arten zeigen einen Trichterzug ins mittlere Mittelmeergebiet.

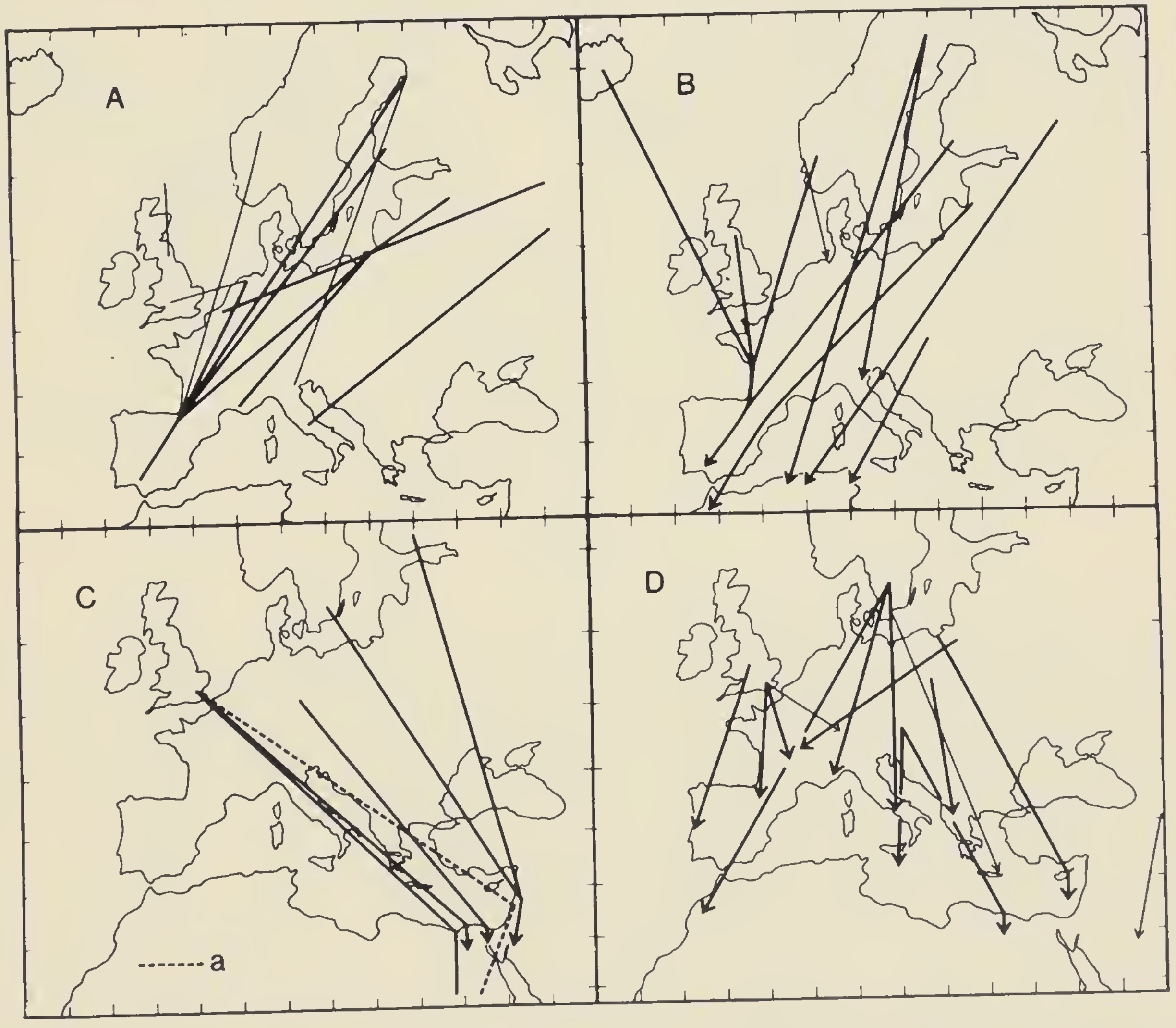
Bei mindestens 14 Arten gibt es eine Zugscheide, die Populationen mit unterschiedlichen Anfangsrichtungen trennt.

Einige Beispiele sollen diese Verhältnisse erläutern. Die Quellen dazu finden sich bei Zink (1973), z. T. auch in unveröffentlichten Unterlagen der Vogelwarte Radolfzell. Alle europäischen Populationen der Feldlerche (*Alauda arvensis*, Abb. 1 A) ziehen, soweit es sich nicht um Standvogelpopulationen handelt, in Richtungen zwischen WSW und SSW. Von Schottland aus mögen auch Richtungen um S möglich sein. An der SW-Ecke der Biskaya treffen sich Populationen sehr verschiedener Herkunft. Die Fernzieher überwintern in Westeuropa westlich des Rheins und im Mittelmeergebiet. Der Steinschmätzer (*Oe. oenanthe*, Abb. 1 B) gehört zu den Arten, die aus Mittel- und Osteuropa in breiter Front nach SW ziehen. Die Konzentration an der Biskaya-Ecke ist deshalb weniger stark als bei der Feldlerche. In NW-Europa sind SW-Richtungen natürlich nicht möglich. Steinschmätzer aus Island ziehen deshalb zunächst nach SSE, Vögel aus Großbritannien und z. T. auch

Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell, Möggingen, Bundesrepublik Deutschland.

aus Norwegen um S. Sie biegen dann, sobald die geographische Situation es erlaubt, also an der Biskaya-Ecke bzw. in NW-Deutschland, in die „richtige" SW- bis SSW-Richtung ein. Steinschmätzer überwintern südlich der Sahara. Richtungsänderungen britischer Vögel an der Biskaya-Ecke gibt es bei vielen Arten (z. B. Abb. 3 A, C und D).

Nur zwei der 89 Arten sind in Europa echte SE-Zieher: Zwergschnäpper (*Ficedula parva*) und Grüner Laubsänger (*Phylloscopus trochiloides*), die beide in Indien überwintern. Die 7 weiteren Arten, die aus West- und Mitteleuropa nach SE wandern, werden im nächsten Abschnitt (Trichterzug) behandelt. Neben den reinen SW- oder SE-Ziehern gibt es einige Arten, die bei gleicher Herkunft recht verschiedene Richtungen einschlagen können. Schilfrohrsänger (*Acrocephalus schoenobaenus*, Abb. 1 D) können von Großbritannien nach Portugal (SSW) oder in die Schweiz (SE), aus Skandinavien nach Spanien (SSW), nach Italien (S) oder nach Kreta (SSE) ziehen.

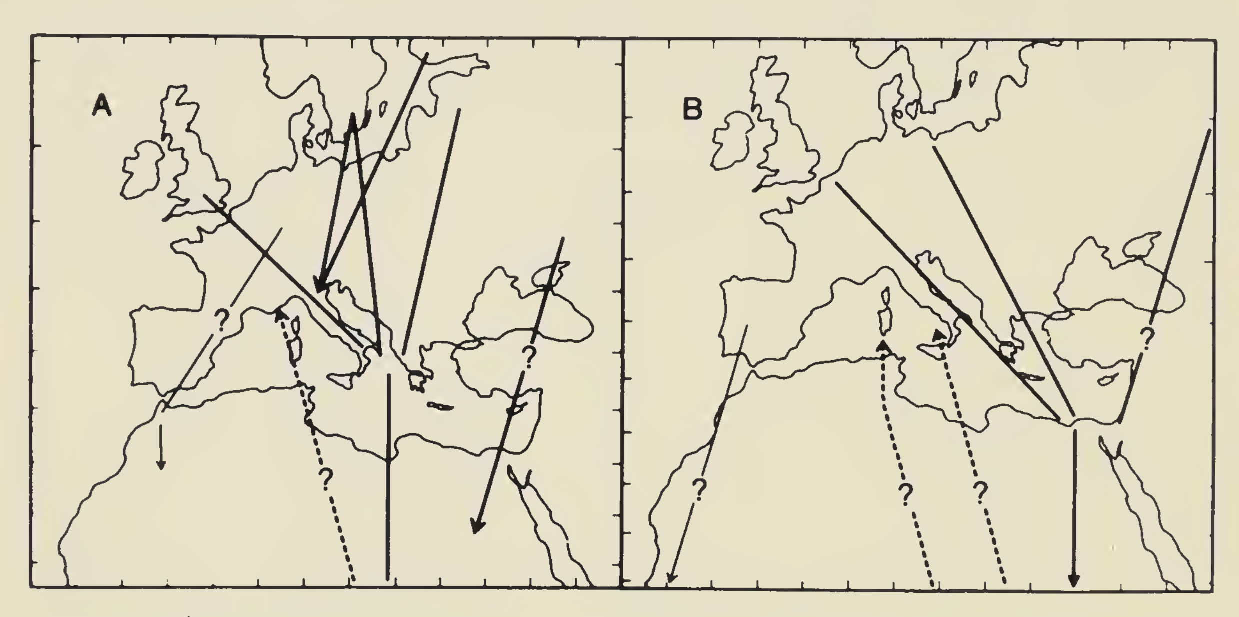


FIGUR 1. Herbstzugrichtungen von A = *Alauda arvensis*, B = *Oenanthe oenanthe*, C = *Sylvia curruca*, D = *Acrocephalus schoenobaenus*. a = Frühjahrszug. Dünne Linien sind nur durch einzelne oder wenige Ringfunde belegt.

Trichterzug

Drei Arten ziehen trichterförmig ins mittlere Mittelmeergebiet, d. h. von Westeuropa mit südöstlicher, von Osteuropa mit südwestlicher Zugrichtung. Der Ostteil des Trichters ist durch Ringfunde meist nur wenig belegt (Beispiel Waldlaubsänger, *Phylloscopus sibilatrix*, Abb. 2 A). Zu den Arten mit trichterförmigem Zugbild gehören aber auch 7 der

9 Arten, die von West- und Mitteleuropa aus nach SE ziehen. Da diese Arten oder mindestens ihre Nominatform ausschließlich in Afrika überwintern, müssen die osteuropäischen Populationen Richtungen um S und bis SSW einhalten. Das gilt z. B. für die Klappergrasmücke (*Sylvia curruca*, Abb. 1 C) und für den Pirol (*O. oriolus*, Abb. 2 B). Beim Pirol ziehen auch die asiatischen Populationen der Nominatform nach Afrika. Die Populationen, die im Trichter nach SE ziehen, müssen die Richtung im Mittelmeerraum oder in Nordafrika nach etwa S ändern. Solche Richtungsänderungen auf dem Zug sind bei fernziehenden Vogelarten weit verbreitet (ZINK 1977, hier Abb. 1 C, 2 A und B, 3 C und D).



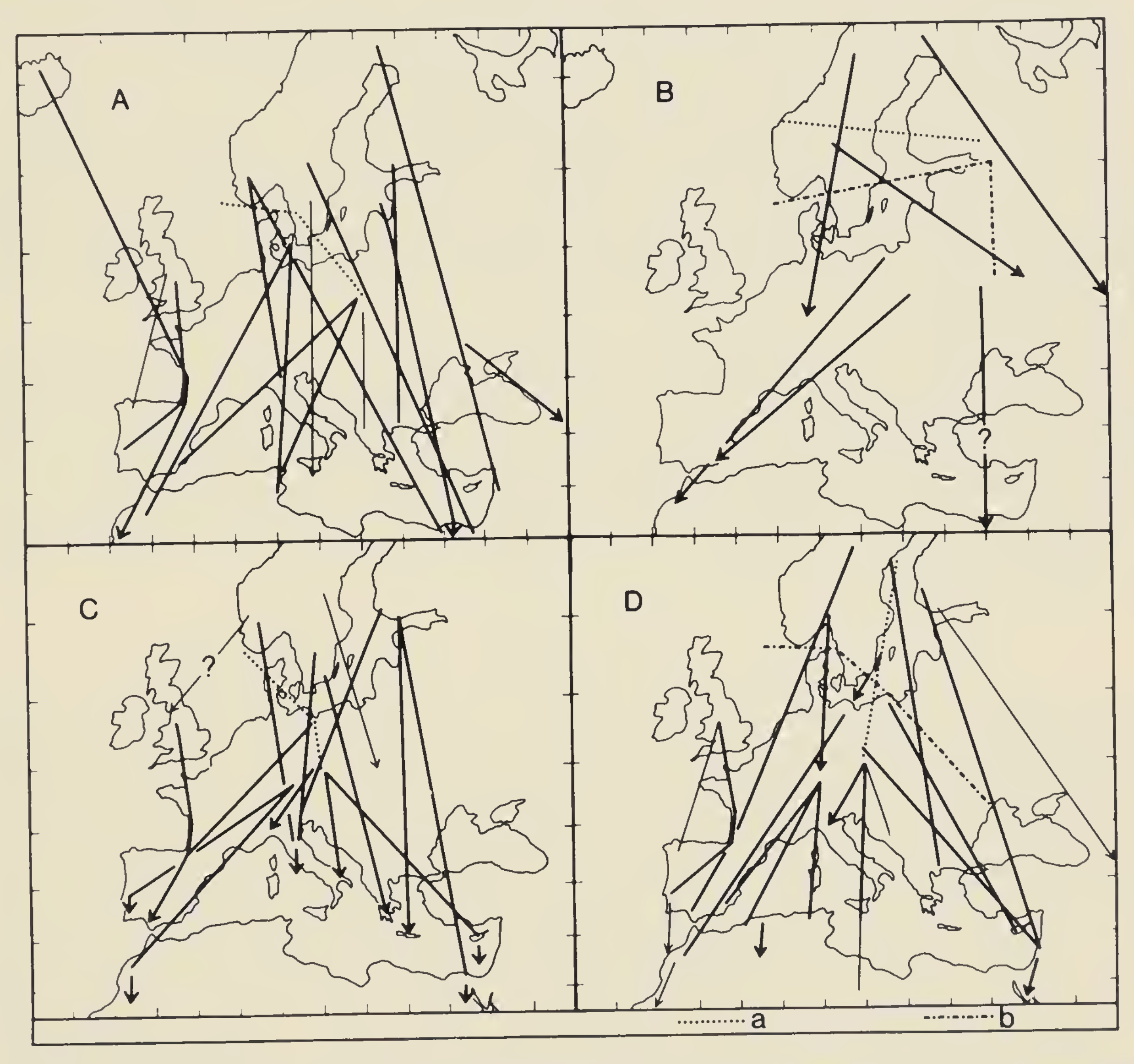
FIGUR 2. Herbstzugrichtungen von A = *Phylloscopus sibilatrix*, B = *Oriolus oriolus*.

Zugscheiden

Das klassische Beispiel für eine Zugscheide stammt vom Weißen Storch (*C. ciconia*). Dieses Beispiel ist durch zahlreiche Funde beringter Vögel besonders gut belegt (SCHÜZ 1962). Auch bei der Mönchsgrasmücke (*Sylvia atricapilla*) ist eine Zugscheide bei etwa 12° E gut gesichert (ZINK 1973). Bei den meisten anderen Arten, bei denen eine Zugscheide existiert, liegt diese weiter nördlich oder östlich, d. h. in Gebieten, wo es meist nur wenige Ringfunde gibt und wo deshalb besonders die Verhältnisse östlich der Zugscheide oft nur angedeutet werden können. Bei der Bachstelze (*Motacilla alba*, Abb. 3 A) ist die Zugscheide zwischen den Populationen Fennoskandiens und denjenigen Mittel- und Westeuropas gut belegt. Der Verlauf südlich der Ostsee kann aber nur vermutet werden, da Ringfunde aus Ost- und SE-Europa fehlen. Der Fund einer in Indien beringten Bachstelze in der Ukraine zeigt, daß es aus diesem Gebiet Herbstrichtungen nach SE gibt. Auch beim Grauschnäpper (*Muscicapa striata*, Abb. 3 C) trennt eine Zugscheide die Vögel Skandinaviens von den Populationen West- und Mitteleuropas. Die Richtungen sind dabei nicht so verschieden wie in anderen Fällen: Während die Vögel westlich der Zugscheide reine SW-Zieher sind, streuen die Wegzugrichtungen skandinavischer und finnischer Vögel zwischen SSW und SSE. Südlich der Ostsee liegt die Zugscheide westlicher als bei der Bachstelze, doch fehlt es wiederum an Funden aus Ost- und SE-Europa.

Die Zugscheide kann in der Nähe einer Rassengrenze liegen, wie bei *Luscinia svecica* (Abb. 3 B), bei der die weißsternigen Blaukehlchen vorwiegend südwestlich, die rot-

sternigen vor allem östlich von S ziehen. Rotsternige Blaukehlchen überwintern aber in geringer Zahl auch in Westafrika, weißsternige vereinzelt auch in Ägypten. Die Zugscheide kann von der Rassengrenze aber auch unabhängig sein, wie beim Zilpzalp (*Phylloscopus collybita*, Abb. 3 D). Vögel der Form *abietinus* ziehen aus Norwegen und Schweden in Richtungen westlich von S, Vögel der Nominatform aus Polen östlich von S. Möglicherweise handelt es sich beim Zilpzalp mindestens im südlichen Teil der Verbreitung nicht um eine echte Zugscheide mit divergenten Zugrichtungen, sondern um ein von W her gesehenes allmähliches Schwenken der Wegzugrichtungen von SW über S nach SE.



FIGUR 3. Herbstzugrichtungen von A = *Motacilla alba*, B = *Luscinia svecica*, C = *Muscicapa striata*, D = *Phylloscopus collybita*. a = Zugscheide, b = Rassengrenze.

Einige Arten, bei denen Zugscheiden zu vermuten sind, wurden in dieser Gruppe nicht mitgezählt. So dürften bei Pirol und Waldlaubsänger (Abb. 2) Populationen vom Westrand der Brutverbreitung in isolierte Winterquartiere in Westafrika ziehen. Genauere Angaben können aber nicht gemacht werden, da Ringfunde fehlen.

Schleifenzug

Richtungsänderungen während des Zuges haben zur Folge, daß das Überwinterungsgebiet nicht auf dem direkten Weg, sondern auf einem Umweg erreicht wird. Dieser

Umweg kann beim Heimzug in einem Schleifenzug abgekürzt werden. Das gilt z. B. dann, wenn SW-Zieher, die südlich der Sahara überwintern und folglich im Herbst in Portugal die Richtung ändern müssen, im Frühjahr über Ostspanien zurückziehen. Ein Beispiel dafür ist das Braunkehlchen (*Saxicola rubetra*). Man spricht dann von Schleifenzug gegen den Uhrzeigersinn. Pirole aus Mitteleuropa ziehen im Herbst über Griechenland nach NE-Afrika (Abb. 2 B). Dort muß die SE-Richtung nach etwa S geändert werden. Auf dem Heimzug wird das Mittelmeer im Durchschnitt etwa 8° westlicher überquert als im Herbst. Hier handelt es sich also um Schleifenzug im Uhrzeigersinn. Ob dabei in Afrika noch weiter nach W ausgeholt wird, als in Abb. 2 B angedeutet ist, muß offen bleiben. Ähnliche Verhältnisse gelten wahrscheinlich für den Waldlaubsänger (Abb. 2 A).

In einigen Fällen wird der herbstliche Umweg auf dem Heimzug nicht abgekürzt, sondern noch vergrößert. Britische Klappergrasmücken ziehen im Herbst über Norditalien nach Ägypten. Die Überwinterungsgebiete liegen im Sudan. Auf dem Heimzug wird noch weiter nach E ausgeholt und das Mittelmeer fast vollständig umflogen. Ähnliches Zugverhalten ist vom Neuntöter (*Lanius collurio*) und vom Schwarzstirnwürger (*Lanius minor*) bekannt.

Diese Beispiele, die vervielfacht werden könnten, zeigen die große Vielfalt der räumlichen Zugmuster europäischer Singvögel. Die genaue Kenntnis dieser Muster ist Voraussetzung nicht nur für Orientierungsversuche, sondern auch für Untersuchungen auf dem Gebiet der Zugphysiologie und für vielerlei Aspekte des Vogelschutzes. Es ist deshalb besonders bedauerlich, daß über die Zugverhältnisse in Ost- und SE-Europa so wenig bekannt ist.

Summary: Patterns of Migration in European Passerine Birds

Bird migration in Europe depends largely on the unequal distribution of the land masses in the Old World and the complicated system of coastlines in Europe. It is also influenced by the fact that Africa extends seven degrees of longitude farther west than does Europe and that the coastal areas of the Atlantic Ocean in Western Europe provide suitable wintering grounds for many species. Strict northsouth-movements are, therefore, exceptions in the migrations of European birds. The paper describes the main autumn directions found in the passerine families (with the exception of the buntings, finches and sparrows) and emphasizes such peculiar patterns as broad-front and funnel-shaped migration (Breitfrontzug und Schmalfront- oder Trichterzug), changes in direction during migration, migration divides (Zugscheiden), and loop migrations (Schleifenzug). The knowledge of these patterns is essential not only for orientation studies but also for studies on environmental physiology and for many aspects of bird protection. It is, therefore, deplorable that our knowledge of the migration patterns in eastern and southeastern Europe is so poor.

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The Influence of Global Climatological Factors on the Evolution of Bird Migratory Pathways

Sidney A. Gauthreaux, Jr.

Introduction

The persistence of animal populations is dependent in large part on the ability of individual organisms to move so that they can reproduce in the most appropriate place at the most appropriate time. All populations are spatially fluid in some measure because movement is a fundamental biological response to adversity (Taylor & Taylor, 1977). Every organism must retain the ability for it or its descendents to change location eventually or face extinction. Evolution will therefore favor all traits that serve to maximize the expectancy of arriving and surviving to breed, for example, the ability to disperse or migrate, the ability to survive the dangers of dispersal and migration, and the ability to find, or arrive in, the new habitats (Southwood, 1977). It is reasonable to expect that the seasonal climatic factors that render a habitat favorable or unfavorable are the same factors that influence the dispersal and migration of organisms to and from that habitat, respectively. It also follows that the motions of the atmospheric medium have imparted some directionality to dispersal and migratory flights and at the same time have played a role in the phenology of the flights. Although previous interest has been shown in the adaptation of passerine migratory routes to general wind circulation (e.g., Bagg et al., 1950; Lowery, 1951:454–458; Williamson, 1955, 1969; Evans, 1966; Graber, 1968; Able, 1972; Richardson, 1976) mine is the first attempt to integrate global atmospheric patterns with continental migration patterns in an effort to better understand the evolution of migratory pathways.

Recent empirical and theoretical investigations of the flight energetics of migratory birds suggest that the longest non-stop flights of birds are physiologically possible only if the birds are aided, or a least not hindered, by the wind (Tucker, 1975). The large number of migration studies that show that migrating birds attempt to maximize the following wind component whenever possible further supports the notion that the movement of the atmosphere has had an important influence on the flight directions and migration routes of birds flying between their breeding and nonbreeding areas.

In the analysis that follows I examine the relationships among global wind circulation, topography, and the patterns of bird migration. Because of space limitations, I will emphasize these relationships only in North and Central America and make limited comments about other regions of the world. A more detailed presentation will appear elsewhere.

Methods

The climatological data for this analysis were taken from a numer of sources (Borchert, 1953; Aleman & Garcia, 1974, Bryson & Hare, 1974; Court 1974; Hare & Hay, 1974; Boucher, 1975; Portig, 1976; the Climatic Atlas of the United States, and

Department of Zoology, Clemson, South Carolina, USA.

the Atlas of Climatic Maps-Canada). Because of the importance of the atmospheric circulation, I have emphasized patterns of barometric pressure (1000 mb) and surface winds in the analysis. The winds at an altitude of 0.5 km closely the 1000 mb isobars, lines connecting points of equal barometric pressure (see HUMPHREYS, 1940). These climatic patterns of barometric pressure are based on nearly 50 years of observations at hundreds of weather stations throughout the northern portion of the Western Hemisphere. I have used only those pressure and wind patterns during periods of migration, April and May in spring (Figure 1) and September and October in fall (Figure 3). In these figures the directions of surface winds are indicated with arrows, and many of these data are based on an analysis of monthly resultant wind directions and speeds at 00:00 GMT over a period of 13 years at 77 weather stations in the United States (GAUTHREAUX, in preparation).

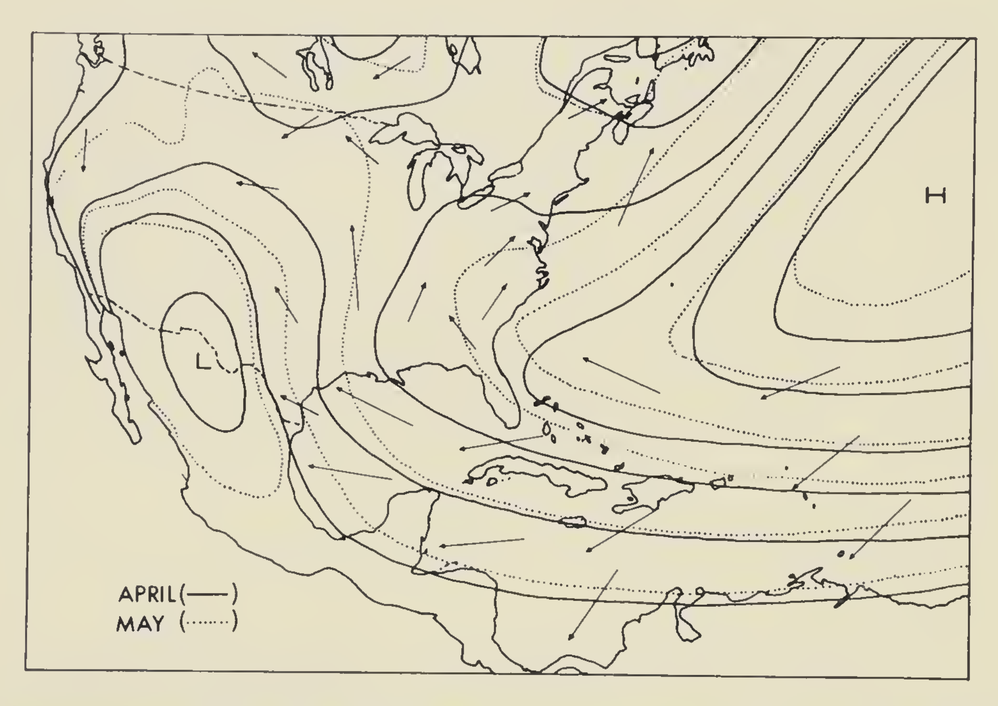


FIGURE 1. The distribution of sea-level barometric pressure patterns in spring. The continuous and dotted lines connect points of equal pressure and are for the months of April and May, respectively. The arrows indicate the resultant direction of the surface winds.

The bird migration data for this analysis were gathered from a number of sources (LOWERY, 1951; DRURY & KEITH, 1962; BELLROSE & GRABER, 1963; HASSLER et al., 1963; NISBET, 1963; BELLROSE, 1964, 1965; DRURY & NISBET, 1964; LOWERY & NEWMAN, 1966; NISBET & DRURY, 1967a, 1967b, 1968; GAUTHREAUX, 1968, 1971, 1972, 1978, in prep.; GRABER, 1968; MONROE, 1968; BUSKIRK, 1971; FORSYTH & JAMES, 1971; NEWMAN & LOWERY, 1971; RICHARDSON, 1971, 1972, 1974, 1975, 1976; RICHARDSON & GUNN, 1971; ROBERTSON & OGDEN, 1971; ABLE, 1972, 1974a, 1974b; HILDITCH et al., 1973; WILLIAMS et. al., 1977a, 1977b). All of these citations refer to studies of primarilly passerine migration by direct visual means (moon-watching or the ceilometer technique), by radar (surveillance or tracking radars), or by a combination of the two. The darkened wedges in the circles in Figures 2 and 4 represent the mean direction of passerine migration as reported by the authors plus or minus 30°. In certain cases when the author indicated two rather distinct directional tendencies, each has been included in the circle.

Results

Figure 1 shows the average sea level barometric pressure patterns and surface wind direction for much of North and Central America for the months of April and May. Just above the boundary layer in the lower troposphere where the effects of surface friction are minimal, the flow of air is parallel to the isobars and is termed the geostrophic wind. It is a good approximation to the observed wind at heights of about 500 m at latitudes outside the equatorial zone (above 10°N). As one moves downward through the boundary layer toward the earth's surface frictional drag causes surface winds to move across the isobars in the direction of low pressure at an angle of about 15° over the oceans and 30 ° over land. Near the surface, winds blow at reduced speeds, and because of daytime heating and turbulence the geostrophic winds are generally slower during the day than at night. At night when the surface air stops rising and the boundary layer becomes thinner, horizontal air movement at 500 m becomes smooth and fast. Thus in spring at night, the mean flow of air at a height of approximately 500 m is quite close to the isobaric lines portrayed in Figure 1. This is the motion of the atmosperic medium within which most passerine birds migrate. How do these patterns relate to the mean directions of nocturnal passerine migration?

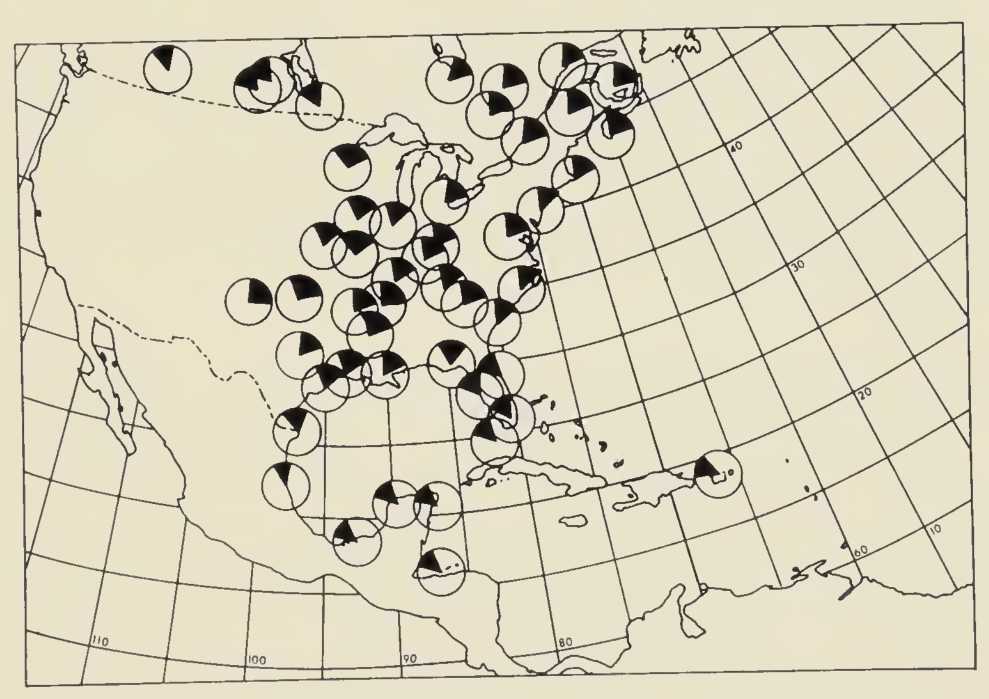


Figure 2. The directional tendencies of nocturnal passerine migration spring. The circular plots show the predominant direction of migration for a given area. The thickness of the darkened wedge reflects the variability in direction of major movements.

The mean directions of nocturnal passerine migration in spring are given in Figure 2. As can be seen, there is in general agreement between the average directions of air flow at 500 m altitude and the mean directions of passerine migration. South of 20°N the direction of migration is strongly biased toward the west-northwest and northwest. In Florida and along the northeastern Mexican coast there is a tendency for migration to shift more toward the north, and near 30°N the movement of birds is somewhat east of north. These changes in the average direction of migration closely parallel the changes in the orientation of the isobars. At increasing latitudes in the eastern third of the continent migration shifts

more toward the northeast and east-northeast. This is generally in keeping with the direction of the isobars. It should also be noted that the velocity of the geostrophic winds increases with increasing latitude to a maximum in the midlatitudes (40-50°N), the zone of maximum baroclinity (BOUCHER, 1975:49). In the central United States passerine migration proceeds generally northward and then turns towards the northeast in the vicinity of the Great Lakes and toward the northwest west of the Great Lakes. This interesting diversion is also present in the wind patterns, and the generation of the cold easterly circulation over the Canadian western plains in spring has been discussed by RADDATZ & KHANDEKAR (1977).

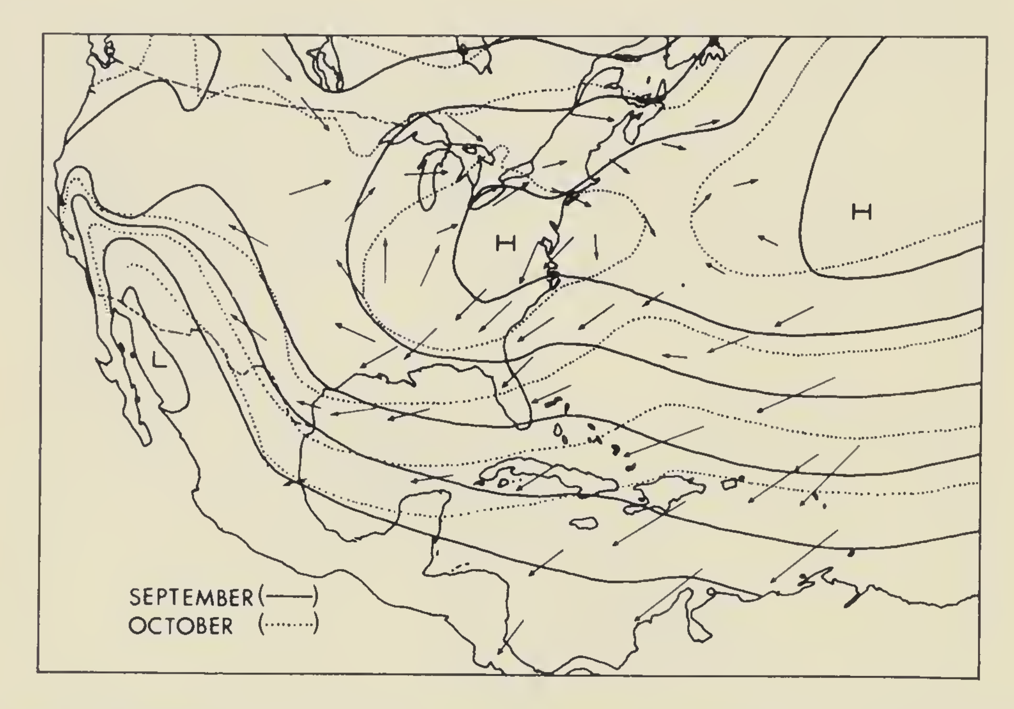


FIGURE 3. The distribution of sea-level barometric pressure patterns in fall. The continuous and dotted lines connect points of equal pressure and are for the months of September and October, respectively. The arrows indicate the resultant direction of surface winds.

In the fall (September and October) the average sea level barometric pressure pattern and surface wind directions for most of North and Central America show a change, particulary north of latitude 25°N. A high pressure cell is positioned over the eastern United States, resulting in northeasterly surface winds from New Jersey through the southeastern states to Louisiana. The geostrophic winds in this general area are easterly and east-northeasterly. This is in part a result of the northward advancement of the northeasterly trade wind belt. In the central southern Canadian region surface winds are from the northwest, and geostrophic winds range from northwest to westerly.

The general flow of passerine bird migration in the fall (Figure 4) shows considerably less agreement with geostrophic wind patterns than in spring. Although there is rather close agreement between mean wind direction and mean migration direction in the eastern and southern United States and in the central southern Canadian regions, there are noticeable deviations of the mean migration directions from the average geostrophic wind direction in the central and extreme northeastern United States, in Florida, and in the Canadian Maritime Provinces. The general impression is that most migration north of 35°N and west of 85°W is directed southeastward or south-southeastward to the

Appalachian Mountains and the Atlantic Coast. East of the mountains the migrations parallel the coast and mountain chain and move toward and along the northern coast of the Gulf of Mexico and down the Florida peninsula. The migrations from the northeastern United States and the Canadian Maritimes over the western Atlantic Ocean have basically favorable winds.

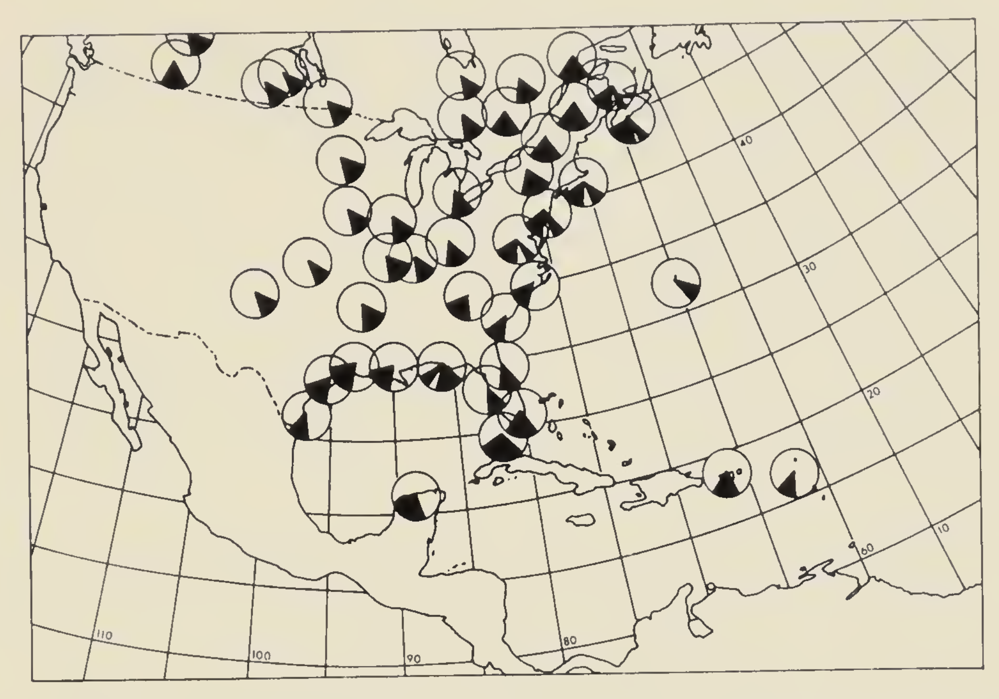


Figure 4. The directional tendencies of nocturnal passerine migration in fall. The circular plots show the predominant direction of fall migration for a given area. The thickness of the wedge approximates the usual variability in direction. When two major directional tendencies exist for an area, they are both indicated.

Discussion

The seasonal migrations of birds appear to follow a general eliptical pattern in North and Central America, and this is in keeping with the general zonal circulation of the atmosphere (easterlies below 30°N and westerlies above 30°N). As the heated and expanded air of the equatorial regions overflows to higher latitudes it is deflected by the rotation of the earth. That portion that goes north changes from an east wind near the equator to a southeast, south, southwest, and, finally at about latitude 35°N, a westerly wind. Thus in spring the northward migrations of birds from their tropical wintering grounds are biased in direction toward the west by the prevailing easterly winds, and in general follow the influx of heated and expanded air northward into North America. The directions of spring migrations are closely correlated with the geostrophic wind patterns over most of the continent in spring. In fall the southward migrations appear to be initially biased in direction toward the east by the prevailing westerly winds, but in eastern Canada and in the eastern United States the flow of migration is oriented toward the southwest paralleling the Atlantic Coast. The agreement between the patterns of geostrophic winds and the average directions of migration is not as pronounced as in spring, and several factors are probably responsible.

Geostrophic winds are not favorable in the central United States and in the northeastern United States in fall. In the former region the winds blow northward on the average, and in

the latter region the average geostrophic winds blow eastward and would carry birds out over the Atlantic Ocean. Over Florida in fall, nocturnal migrants following the geostrophic winds would come in from the Atlantic Ocean and then move westward over the Gulf of Mexico. In these regions it is clearly adaptive for migrants to wait for favorable winds blowing in the general direction of their destination. There are nonetheless numerous cases of nocturnal migrations underway in seasonally inappropriate directions following the generalized geostrophic flow (e.g., reversed migration at night).

The geostrophic circulation patterns as presented are theoretical and are based on the distribution of barometric pressure patterns during the spring and fall over a period of many years. In addition, the winds as diagrammed do not take into account the eastward progress of cyclonic and anticyclonic system over the North American continent. The actual overall pattern of atmospheric circulation over much of the United States and Canada resembles the monsoon circulation or seasonal wind.

If the term monsoon is extended to include all winds whose prevailing directions and velocities undergo distinct alterations as a result of seasonal changes in temperature because of widespread heating and cooling, then this circulation pattern is nearly universal (Humphreys, 1940).

However, it is generally thought of in connection with only those places where it is most strongly developed, and especially where the seasonal winds are more or less oppositely directed (India and southeastern Asia, portions of Africa, Australia, and the Caspian Sea). In the United States the major monsoon effects are in the eastern portion, where the prevailing winds are northwest in winter and southwest in summer, and in Texas, where the prevailing winds are also northwest in winter, but southeast in summer (Humphreys, 1940). The reversal of wind direction in south-central Canada is also suggestive of a monsoon pattern.

Because monsoons depend upon seasonal temperature contrasts between land and water, winds of this class must be most pronounced where such contrasts are greatest, that is, in temperate regions. During the spring the number of cold fronts that penetrate the North American continent and reach the Gulf of Mexico decreases, and consequently the advancement of moist, tropical air into much of North America is facilitated. This pattern of increasing southerly flow and decreasing northerly flow is rather typical of the advancement of the monsoon in other regions of the world. The spring migrations of birds from their wintering areas takes place with the advancement of the tropical air mass.

During the fall the number of cold fronts that penetrate the continent and reach the Gulf of Mexico increases, and the moist, tropical air mass is replaced by a cold, dry air mass. A northerly flow of air comes to dominate much of the North American continent during the winter months, and freezing temperatures are frequent, a situation similar to the retreat of the monsoon in other areas of the globe. The fall migrations of birds from their breeding areas are associated with the increasing frequency of cold fronts and the movement of cold air masses southward.

The relationship between monsoon circulation and the directions and timing of bird migrations is probably found in a number of geographical regions throughout the world. Moreau (1972:31–44) has discussed bird migration into and from Africa in relation to wind patterns, and Myres & Apps (1973) have examined with radar the migration of birds over the south coast of China. They found that the flights were directed toward the

northeast in spring and toward the southwest in autumn. These directions and the timing of the flights are in accordance with the monsoon atmospheric circulation typical of that region. Likewise, in Australia, another continent having a monsoon circulation, NIX (1976) has shown that the timing and direction of migration are closely tied to the timing and atmospheric circulation of the monsoon.

LACK (1960) has emphasized that climatic conditions were and are a major selection pressure in determining the migration and breeding seasons of bird species, and WILLIAMSON (1953) has suggested that migration seasons may have evolved to coincide with periods which have optimal weather and to avoid those periods which have less favorable conditions. With regard to the phenology of migration it should be stressed that it is the action of modifying factors (climatic) that largely determines the observed annual variations in arrival and departure dates and other migration phenomena (WIESE, 1974). Climatic factors (e.g., large scale wind and temperature patterns) can have a direct effect on the phenology of migration (GAUTHREAUX & LEGRAND, 1975), or these factors can also advance or retard migration by their effect on the phenology of vegetational change (SLAGSVOLD, 1976). Many authors have repeatedly shown the influence of temperature on the phenology of migration as evidenced by the rather close agreement between isochronal lines and isotherms on spring migration maps (DORST, 1962), but there has been little emphasis on the contribution of atmospheric motion to the isochronal patterns. Both wind and temperature are of course closely interrelated in that winds blowing from warmer regions of the globe raise temperatures while winds blowing from colder regions lower temperatures. Unlike earlier authors (cf. LACK, 1960; DORST, 1962:240), more recent studies on the influence of weather factors on bird migration have found that wind is one of the most influential variables that explains the greatest portion of the day-to-day variation in the amount of bird migration, and as expected, many studies have found that temperature variables are nearly as important (GAUTHREAUX, in press; RICHARDSON, in press). Thus it appears that both the phenology and the orientation of bird migration have been and continue to be influenced by the general atmospheric circulation, and changes in the pattern of atmospheric circulation have important climatic and ecological effects (see LAMB 1975; WILLIAMSON, 1975, 1976).

Acknowledgments

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SYMPOSIUM ON
ORIENTATION IN MIGRATORY BIRDS

10. VI. 1978

CONVENERS: ST. T. EMLEN AND W. WILTSCHKO

Modifying Influences of Environmental Factors on a Time-distance-program in Bird Migration

HELMUT KLEIN

There is evidence indicating that some first year migrants might find their winter quarters on the basis of vector orientation i.e., by migrating in a specific direction for a given time. This supposition is supported by the results of field and laboratory experiments, recently reviewed by EMLEN (1975) and GWINNER (1977). But as GWINNER (1977) has pointed out, the model is still open to criticism especially since a simple time-distance-program is probably not always accurate enough to terminate migration in the natural winter quarter. For this reason, and because there is hardly any important biological process that is controlled by one factor only, one would expect that mechanisms exist which compensate for inaccuracies caused by internal or external factors. The purpose of this paper is to outline mechanisms that might improve the accuracy of a time-distance-program.

Disturbing influences from the environment

The most obvious environmental influence on bird migration is that of the wind. One must, however, discriminate between winds that are highly predictable, like the trade winds, and unpredictable winds caused by low or high pressure cells in mid latitudes. It seems likely that the effects of predictable winds are incorporated in a time-distance-program, and since their directions are mostly perpendicular to the direction of migration, they are of minor importance with respect to distance measurement.

The influence of winds during flight may be reduced by two reactions. (1) Radar observations of BRUDERER (1971), STEIDINGER (1972) & RICHARDSON (1976) and others suggest that birds tend to avoid altitudes with unfavourable winds during migratory flights. (2) Radar studies also indicate that flying birds compensate for about $^1/_3$ to $^3/_4$ of the effect of winds on direction of migratory flight by altering air-speed (BELLROSE 1967, BRUDERER 1971 & EMLEN 1972).

To assess the maximum remaining influence of the winds of a low- or high-pressure cell I made the following computations. I assumed a large, round, low-pressure system 2800 km in diameter with winds of 50 km/h at flying altitute. A bird like *Sylvia borin* was considered which flies for 2.5 hours per night, a realistic average confirmed by many laboratory experiments and banding results. I assumed further that the bird might enter the wind system so that a maximal headshift occurred and that the bird would not compensate for the influence of wind on its migrating direction, but that it would compensate $^1/_2$ of the wind's effect, by decreasing its ground speed. The calculation then should give the maximal influence of the wind of a high or low pressure system. I found that the maximal headshift would be about 900 km, which is only $^1/_{10}$ of the migration distance for an extremely long distance migrant. Whereas it is $^1/_3$ of the distance of a short distance migrant like a South-German *Sylvia atricapilla.* In addition it should be recognized that

Max-Planck-Institut für Verhaltensphysiologie, 8131 Andechs-Erling/Obb., Bundesrepublik Deutschland.

long-distance migrants have a better chance to encounter another wind system with opposite effect. From this I concluded that the influence of winds on the migrating distance of a long-distance migrant is not very important, whereas it is of great importance to a short-distance migrant.

This led to a consideration of some existing information from a new point of view. It has been known, for a long time, that short-distance migrants are more responsive to weather conditions than long-distance migrants (compare KLEIN et al. 1973, CZESCHLIK 1976). So far this phenomen has been discussed only with respect to its importance in escaping inclement conditions such as cold or snow to which short distance migrants are in general more often exposed than long distance migrants. Now it seems clear that if short-distance migrants use vector orientation it is important for them, in contrast to long-distance migrants, to avoid migratory flights in stormy weather since such could lead to drastic errors in migration distance.

There are other factors that influence the measurement of distance as strong winds, heavy rain or extreme darkness at night as they suppress migration. (For references see LACK 1960, CZESCHLIK 1976 & RICHARDSON 1978). Delays caused by such interposed stays could be compensated by increased migratory activity either during the following nights or even during the day.

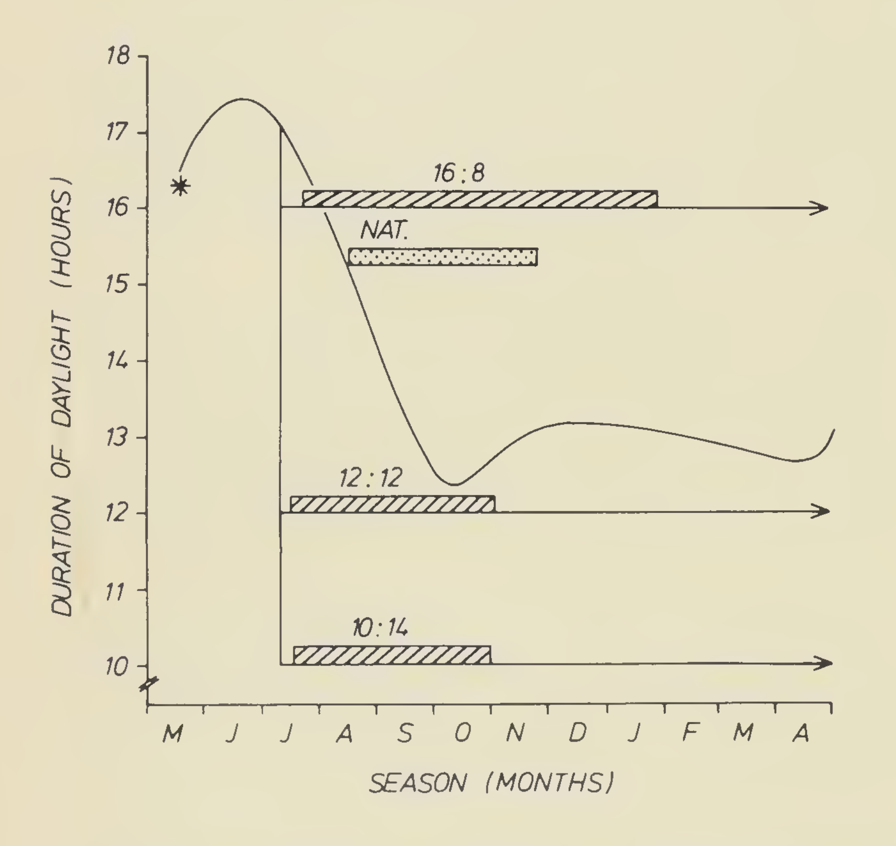


FIGURE 1. The photoperiod experienced by a free-living *Sylvia borin* of the South-German breeding population in the course of the year (continuous line), and experimental photoperiods after July 10th. The dotted bar indicates the time of natural migration, the lined bars indicate time with Zugunruhe in the experimental groups. Experimental data from BERTHOLD et al. (1972); data on migration from KLEIN et al. (1973) and KLEIN (1974).

In this context it is important to recognize that migrating birds seem to fly neither every night during their migration period (BERTHOLD 1978) nor during the entire night. We know from banding stations that *Sylvia* warblers are often retrapped at the same station during the same season. Activity recordings in the laboratory have shown that birds have nights with almost no Zugunruhe and with respect to single nights it is known that Zugunruhe rarely persists through the entire night. From this it may be concluded that there is time for compensatory migratory activity by increasing the flight time per night as well as by adding nights of migration. Indeed CZESCHLIK (1976) presented data from

laboratory experiments with *Sylvia* species suggesting that very dark nights in which there is a drastic reduction in Zugunruhe are followed by nights with excessive Zugunruhe when the light intensity increased. Moreover the activity is increased during the light time of the following day, which might reflect motivation for migration during daytime.

Correcting influences from the environment

Photoperiod

There are also environmental factors that might improve the accuracy of the distance measurement. Here I might mention first a possible influence of day length (photoperiod). Day length influences circadian and circannual clocks in birds in several ways (see ASCHOFF in this volume). I hypothesize that a bird has an expected value for photoperiod in every season which is coupled to a circannual clock and which is identical with the photoperiod that it naturally experiences in the course of the year. If the expected value is different from the one measured the circannual clock makes correcting phase shifts. In this context it should be mentioned that short photoperiods break photorefractoriness in summer and autumn (FARNER & LEWIS 1971) and that relatively short days have an accelerating effect on juvenile development before autumn Zugunruhe (BERTHOLD et al. 1970; GWINNER et al. 1971) This can be interpreted as an advance shift of the circannual clock, bringing the bird into a physiological state that corresponds to the short photoperiod to which it is exposed.

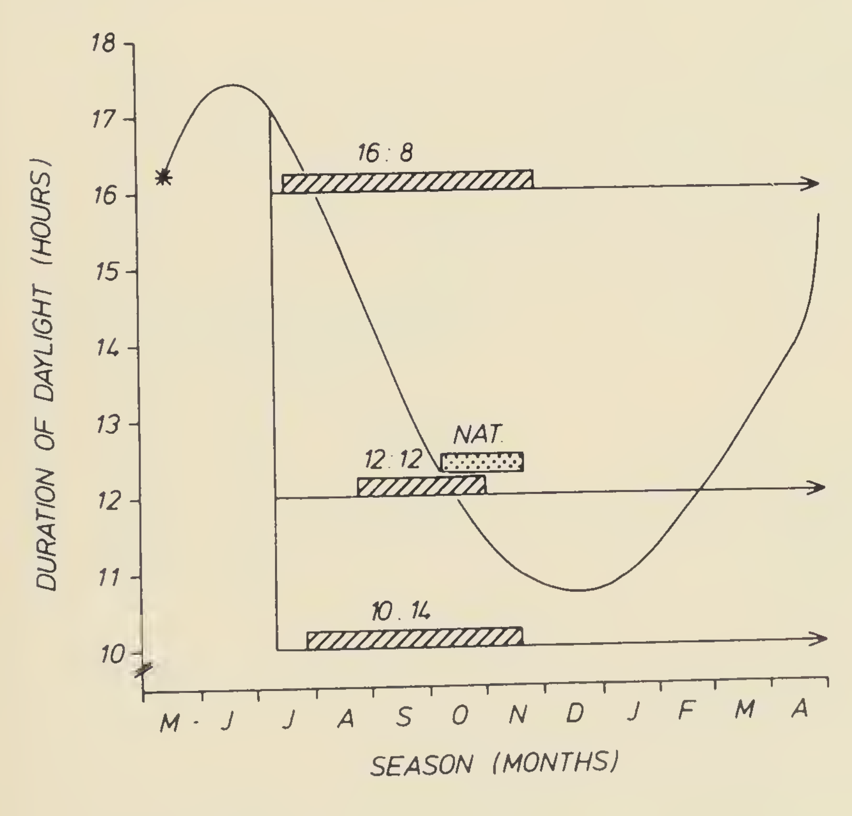


FIGURE 2. Same as Fig. 1 for *Sylvia atricapilla*.

For the following discussion of photoperiodic influences on autumn migration I use data from BERTHOLD et al. (1972). Fig. 1 shows the natural seasonal variations of the photoperiod experienced by a *Sylvia borin* of the South-German breeding population, together with the time of natural autumn migration. It furthermore gives the periods of Zugunruhe for 3 experimental groups of warblers. These birds were kept from hatching until July 10th under natural photoperiodic conditions and then transferred into 16 : 8, 12 : 12 or 10 : 14 respectively. This transfer resulted in all cases in a shortening of the

photoperiod. As a consequence in all 3 groups Zugunruhe started earlier than natural migration would have started. The groups in 12 : 12 and 10 : 14 started even earlier than the group in 16 : 8. Experiments made with *S. atricapilla* produced similar results (Fig. 2). GWINNER et al. (1971) obtained comparable data from two groups of *Phylloscopus trochilus* held on LD 12 : 12 and 18 : 6, respectively from May 24th onwards. In summary, these reactions to short photoperiods in summer can be interpreted as mechanisms that advance the onset of fall migration and, hence, improve its precision if the internal time program is late.

After the warblers have started autumn Zugunruhe, i.e. after they have come into the physiological state of migration, they ,,expect" to experience shorter days as a consequence of migration (see Fig. 1 and 2). If the experienced photoperiod is longer than the on ,,expected" this would indicate that they have not flown far enough. Therefore the circannual clock should be delayed in response to long photoperiods. Hence the birds should stay longer in migratory condition, so that they would migrate longer and consequently for the correct distance. In fact the *S. borin* and *S. atricapilla*, held in 16 : 8, showed extremely long periods with restlessness, while the others, finding themselves already in relatively short days, ceased restlessness earlier. Here we might have an effect that extends migration if the birds are not at the right latitude at the right time.

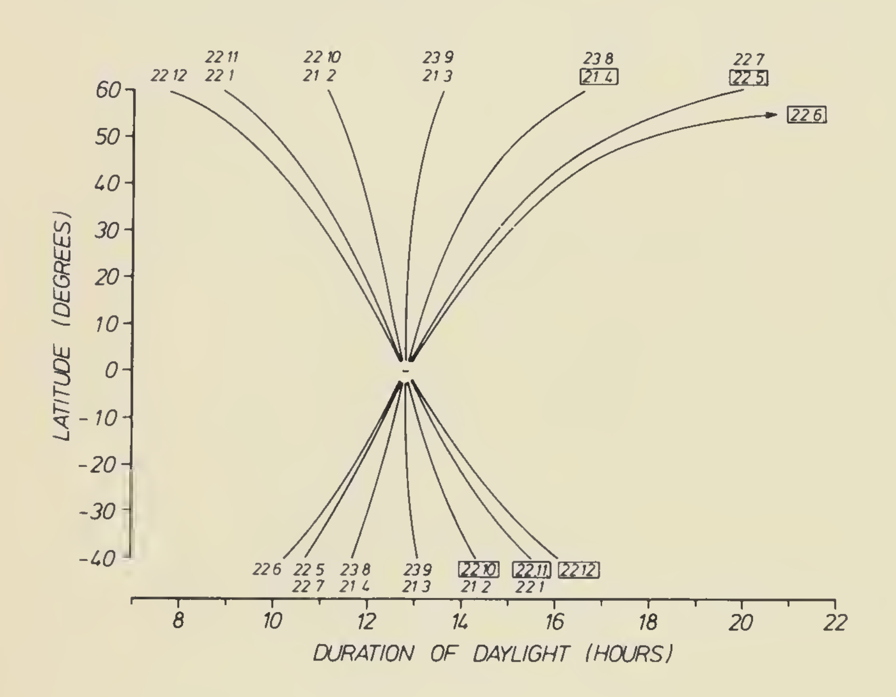


FIGURE 3. Duration of daylight including civil twilight as a function of latitude for selected seasons. The dates during spring migration seasons have boxes on top of the curves. Those of autumn migration have boxes at the bottom of the curves.

So far photoperiodic effects on the beginning and maintenance of migration have been discussed. For the following evaluation of the influences of day length on the termination of migration two relationships must be recognized: (1) As Figure 3 shows, the photoperiod has a clear and sometimes strong N-S-gradient during most seasons. As the seasons of autumn and spring migration are of special interest here, the selected dates for the curve in Fig. 3 have a box around them. We see that during both migratory periods a bird encounters the longer photoperiods, the farther it goes during the later part of its migration. Fig. 4 demonstrates this for *Sylvia borin*.

(2) Experimental evidence indicates that a transfer of warblers to relatively long days toward the end of the fall migratory season induces an earlier termination of Zugunruhe (KLEIN 1974 and GWINNER 1977). This reversal of the response to a long photoperiod

occurring during autumn migration, coincides with the time at which the birds terminate refractoriness and start to react again with gonadal growth if exposed to long days (FARNER & LEWIS 1971). These effects can, again, be interpreted as a advance shifts of the circannual clock. Under natural conditions such reactions could in effect terminate migration if the time-distance-program led a bird too far.

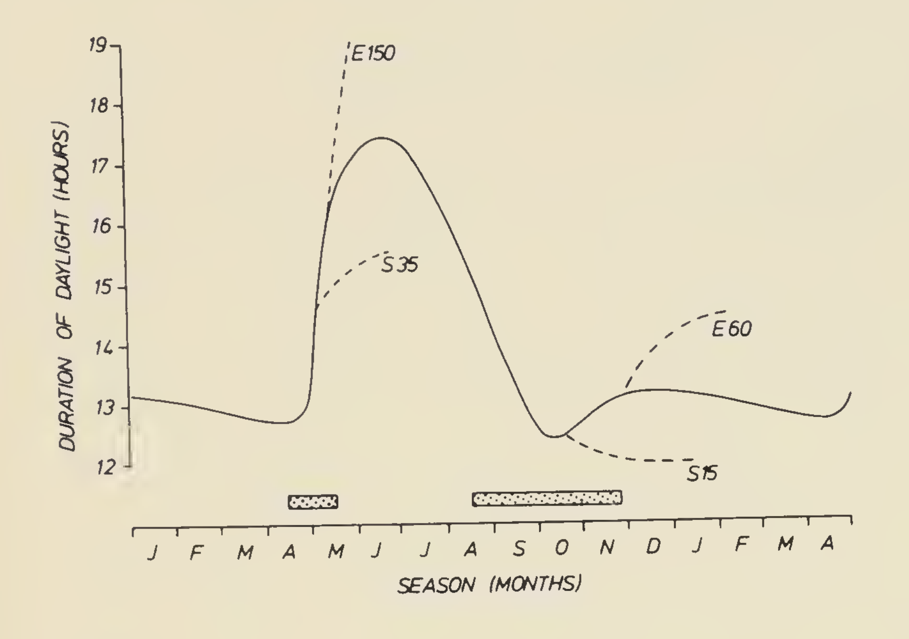


FIGURE 4. Continuous line: photoperiod as in Fig. 1; dashed lines indicate the photoperiods a *Sylvia borin* would experience if it stopped spring migration at 35°N (S 35), autumn migration at 15°S (S 15), or if it extended spring migration 150 km/day (E 150) or autumn migration 60 km/day (E 60). The dotted bars indicate the times of natural migration.

Biotop

Another environmental factor that might influence a time-distance-program is that of biotop. PERDECK (1964) showed that migration of first year Starlings is hardly influenced by the biotops crossed during the middle part of their autumn migration. However during the last part of migration they stop in a suitable biotop earlier than one would expect from a time program, while unfavourable biotops cause longer migration than usual. From this we may conclude that biotops may have extending or terminating effects during the last part of autumn migration.

Conclusions

There are at least several mechanisms by which a time-distance-program could be modified to increase its accuracy. It seems possible that the final precision of such a program together with such modifying mechanisms would be sufficient for vector-orientation.

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Is Bicoordinate Navigation Included in the Inherited Programme of the Migratory Route?

Jørgen Rabøl

The purpose of this paper is to discuss in which way the migratory route of a bird is inherited as a programme, and the question is whether bicoordinate navigation towards a moving goal is included in this programme.

The course of the migratory route could be inherited as a programme in several ways. Fig.1 shows the two extreme possibilities: a) The migratory route is established as compass (one-direction) orientation in relation to one or several extrinsic cues – and the direction could be programmed to shift as a function of the season. b) The other possibility shown is bicoordinate navigation towards a goal which in the course of the season moves down the migratory route. Such a programme involves inherited shifts in the home (sollwert) values of at least two parameters (coordinates) which together form a navigatory grid or map. The programme is assumed to start running at the breeding ground some time after fledging. It is not necessary the assume that the bird is born with a very detailed knowledge of the parameters in the navigation system, but some basic information has of course to be inborn. In the two lower right figures of Fig.1 we have shown – as an example – the shifts in the home values of the two navigational parameters. The first one is the Polaris altitude, the home value of which shifts in the course of the season from a higher to an increasingly low value. In this way the bird will be induced to move South. Instead of Polaris altitude, other possible cues producing a South movement of the goal area could be a decreasing value of the intensity in the Earth's magnetic field, or a decreasing angle of the magnetic inclination. It is more difficult to imagine a programmed shift in the E-W-parameter, but a fixed internal clock running sometimes faster and sometimes slower than 24 hours could be considered. A combination of the two shifting home values shown in Fig.1 will produce a goal area moving down the migratory route shown to the left.

A third possibility is vector navigation (Wallraff 1972), which could be considered as an extension of compass orientation. Vector navigation involves the knowledge of both direction and length of the migratory route. Length per se cannot be programmed, but in a complex manner it is the product of flight speed distribution and time spent migrating. The duration and amount of migratory restlessness in caged migrant warblers is positively correlated with length of the migratory route (e.g. Berthold 1975). It seems most likely that many migrant species are endowed with such an inherited programme based on vector navigation – but this does not necessarily preclude the presence of another and more elaborate system based on bicoordinate navigation towards a moving goal area.

How could we demonstrate the presence of bicoordinate navigation in the inherited migratory programme? Until recently it was claimed that the process of bicoordinate navigation could be demonstrated by the reaction or orientation following a geographical displacement. If the bird compensated for the displacement (i.e. was oriented towards its breeding ground, wintering area, or migratory route) bicoordinate navigation was demonstrated.

Zoological Laboratory, Universitetsparken 15, 2100 Copenhagen, Denmark

As shown in Fig.2 a compensatory reaction could however be established in several ways. It could be bicoordinate navigation towards a goal normally ahead of the trapping position (A), or it could involve a reverse vector from the displaced position (B) to A in connection with a compass orientation vector in the standard direction.

A reverse vector may arise in two different ways: a) The direction or angle of displacement is measured in relation to an extrinsic cue or reference system such as the Earth's magnetic field. Furthermore, the length of the displacement has to be estimated in some inertial way. b) The position of A in a navigatory coordinate system is remembered and compared with the position of B.

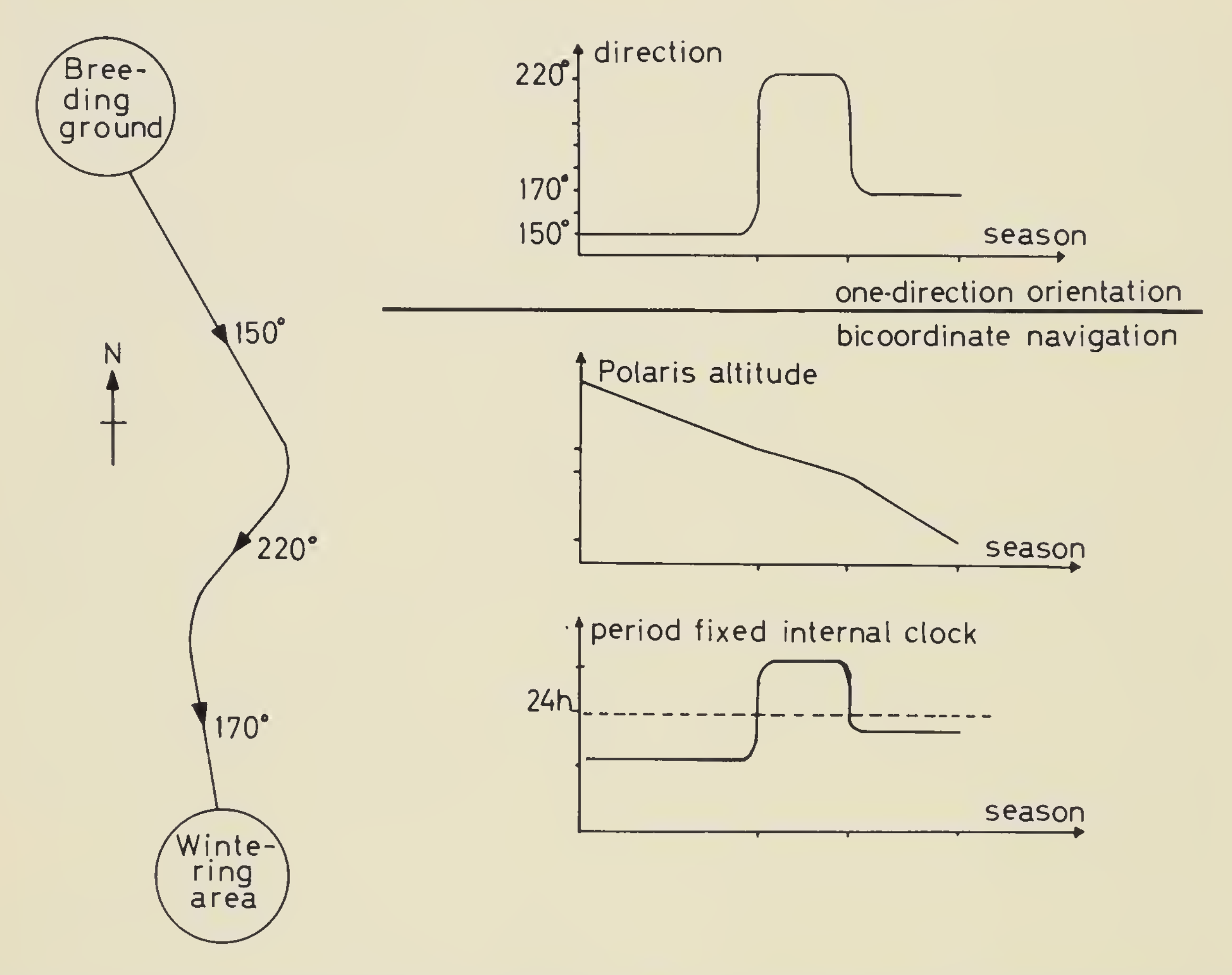


FIGURE 1. In the upper right is shown a programme based on compass (one-direction) orientation. The programme enables the bird to move down the curved migratory route to the left. To the lower right is shown an example of a navigational programme designed for the same purpose.

For carefully selected displacements it should be possible to distinguish between the different models. The idea of such an experiment is a retention of the bird for a long time in the displaced position (B). As supposed by W. WILTSCHKO (in RABØL 1972) the relative strength of the reverse vector (compared to the standard direction vector) should decrease in course of the time elapsed since the displacement. According to this expectation and for most displacements the resultant vector in B will shift gradually and more or less towards the wintering area. This development cannot be distinguished from bicoordinate navigation towards a goal area which in the course of the season moves down the migratory route and ends up in the wintering area. In the case of a very curved migratory route (RABØL 1978) or if the bird is displaced beyond its wintering area the orientation will develop differently according to which programme is employed. Fig.3 could be autumn displace-

ment experiments with Robins (*Erithacus rubecula*) from Denmark to the Canary Islands. As shown to the right in the figure the orientation develops very differently according to the inherited migratory programme in use.

Unfortunately there have been very few well designed displacement experiments with migrant birds. The several investigations concerning pigeon homing and the effect of the outward journey on the departure directions (e.g. Papi et al. 1973, 1978; Fiaschi & Wagner 1976) have shown at least some influence of the outward journey.

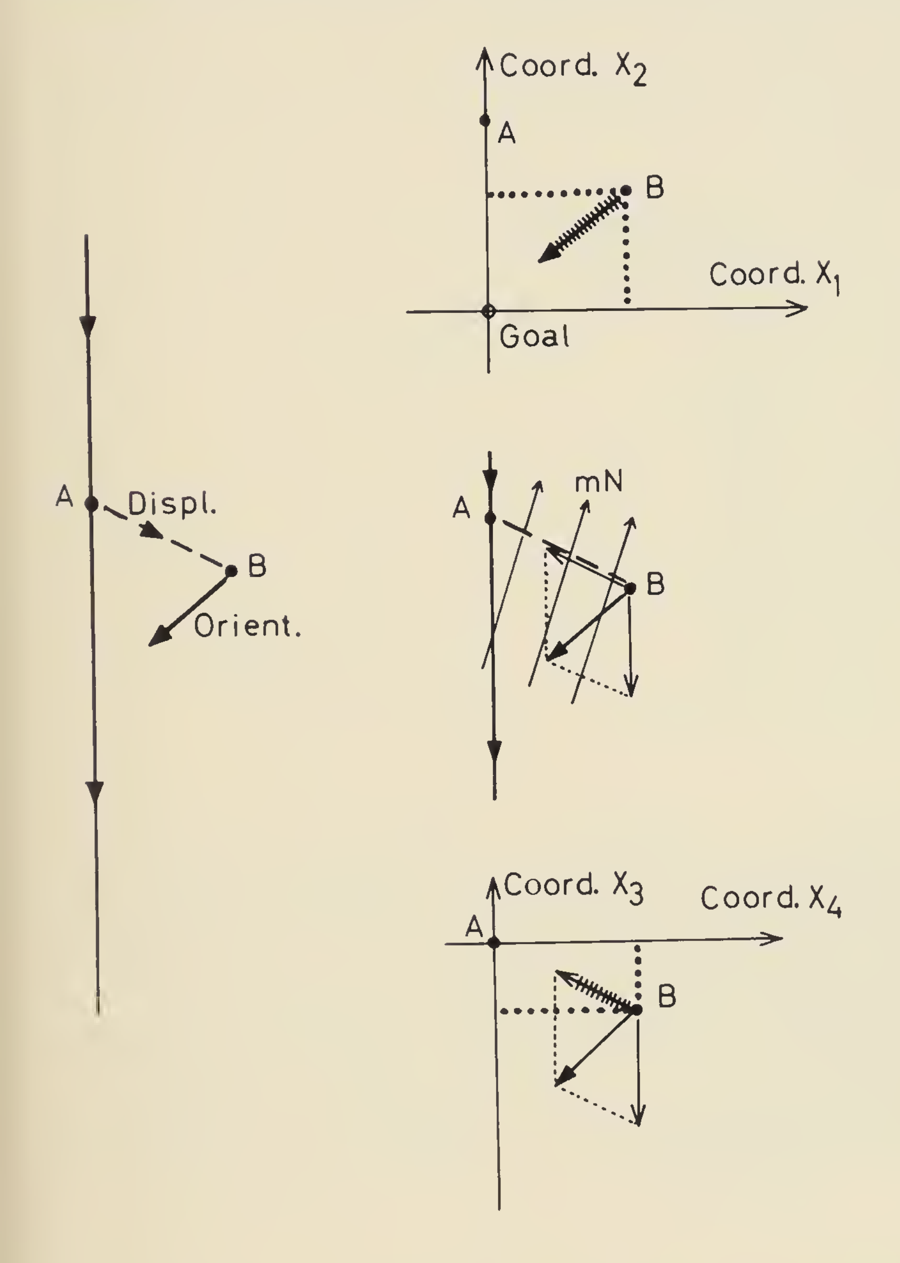


Figure 2. To the left is shown a migratory route directed towards the S (180°). Migrants trapped en route in A are displaced to B (115°). The orientation now shifts from 180° in A to 230° in B. To the right are shown the three explanations for this directional shift. The upper figure shows bicoordinate navigation towards a goal area on the migratory route. In the middle a reverse vector towards A (295°) established during the outward journey in relation to e.g. magnetic North works together with a standard direction vector towards 180°. The resultant vector points towards 230°. In the lower figure the reverse vector from B to A is established as bicoordinate navigation in B. Also in this case the reverse vector works together with a standard direction vector towards 180°.

As discussed by Rabøl (1978) simulated displacements, recovery patterns of ringed birds, and the reverse autumn tracks in Western Europe of Siberian vagrants are all indicative – at least partly – of the presence of bicoordinate navigation towards a goal inherited as a programme.

A final indication of the presence of a navigation system could be the often observed bimodal orientation and/or orientation at right angles to the standard direction in the early and late migratory season, and under conditions of insufficient cue information, or under a presumed low migratory drive (e.g. Emlen 1975, Rabøl unpubl.). Many of these observations are difficult to interpret in terms of compass or vector navigation, and at least some of the observations are indicative of the O-axis hypothesis of Wallraff (1974). This

hypothesis has consequences which can be tested by displacement and retention experiments. At least in long distance migrants we should expect a worldwide navigation system where the coordinates are directed N-S, and E-W – or close there to. The latter coordinate should constitute the O-axis. The departure directions of homing pigeons (WINDSOR 1975, WALLRAFF 1974) do not fit well into this expectation as they converge towards an area NNW of the home site. Perhaps pigeons are navigating in a more local system, or the O-axis is N-S.

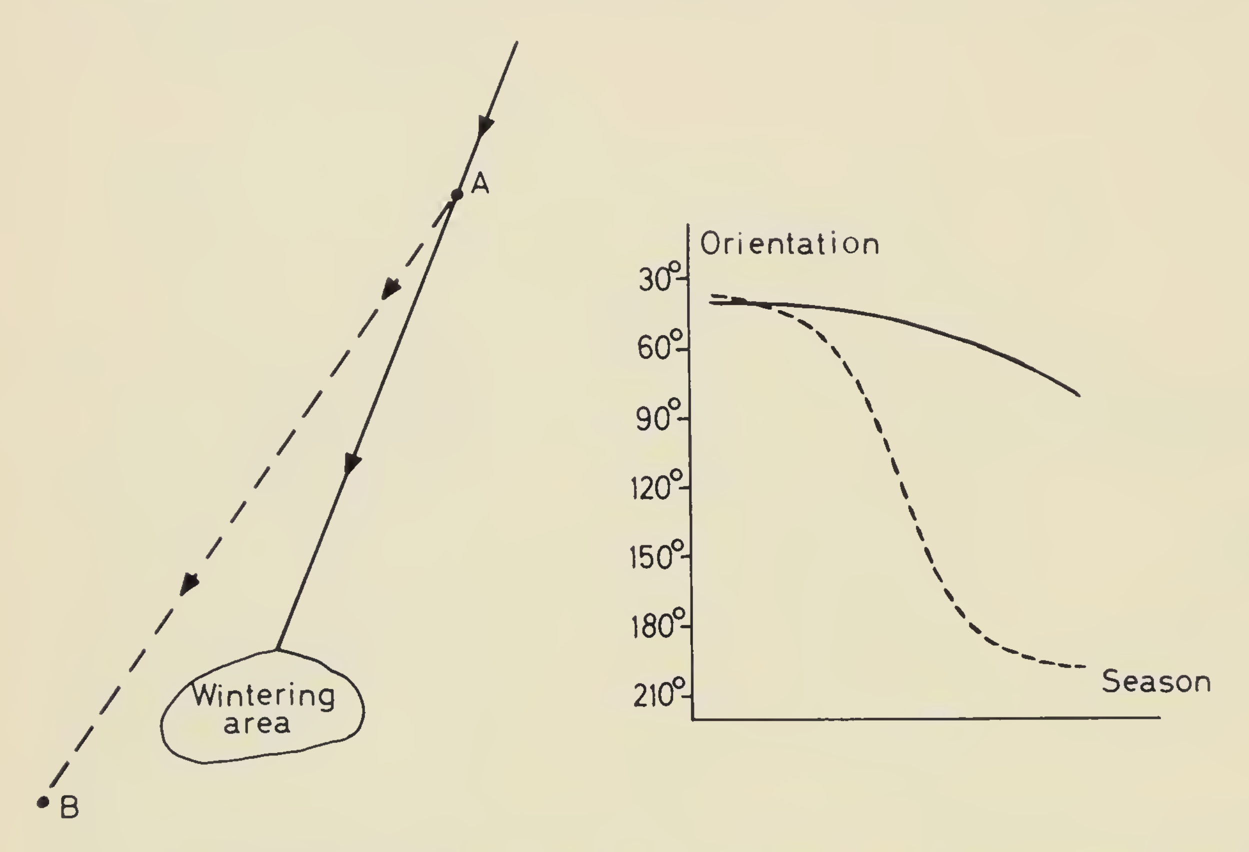


FIGURE 3. The fully drawn arrow to the left is a migratory route directed towards SSW ($202^1/_2°$). Migrants trapped in A are displaced along the hatched line to B (215°), and successive experiments are carried out in B to the end of the autumn migratory season. To the right is shown the development in the orientation in B. If the birds navigate towards a goal area which in the course of the season moves down the migratory route the orientation will shift just slightly clockwise (the fully drawn line). If the orientation in B is a resultant of a standard direction vector towards $202^1/_2°$ and a reverse vector from B to A (towards 35°) which diminishes in strength in the course of the season the orientation in B could shift more or less as denoted by the hatched line. At least in the end of the season the orientation should be more or less southerly and easily distinguished from a ENE navigation towards the wintering area.

In conclusion, there are several indications of a more complex system inherited as a programme rather than just compass or vector orientation. However, the different systems do not preclude each other and the treatment of the birds and the experimental design seem to have profound influence on the results obtained. Bird migration is a complex affair and most questions asked by scientists are so simple and naive that the birds are given no chance of answering in a clear and balanced way.

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Evidence on Migratory Orientation from Radar and Visual Observations: North America

Kenneth P. Able

Introduction

Visual and radar observations of migrating birds have been of vital importance to the development of current understanding of orientation behavior. It was largely data from radar studies which showed that the early models of orientation based on single visual cues (sun or stars) were not sufficient to explain the behavior of migrants in nature. The later realization that considerable redundancy exists in compass and perhaps navigation systems (see Keeton, 1974, Emlen, 1975 for reviews) makes critical observation of free-flying migrants all the more important. Only in the field is the full range of orientation capabilities likely to be expressed. Therefore, it will become increasingly important to base experiments on knowledge of field orientation and to devise experiments that can be performed with free-flying birds.

Field data bear primarily on two aspects of migratory orientation: influences on orientation direction per se, and data concerning the accuracy of orientation. The following discussion will focus primarily on these two areas. Further, I will emphasize nocturnal migration because that is where orientation abilities seem to be put to the greatest test and because most of the available data pertain to night migrants.

Orientation direction

Stars

Studies of migrants in orientation cages have shown unequivocally that birds can use star patterns for compass orientation. Under free-flight conditions, however, visible stars are not necessary for appropriately directed migratory flight (Emlen, 1975, and references cited therein). Apparent selection of an appropriate direction has also been reported under solid overcast (Bellrose & Graber, 1963; Drury & Nisbet, 1964; Nisbet & Drury, 1967; Bellrose, 1967; Cochran, et al. 1967; Gauthreaux, 1971). Indeed, even birds flying within clouds were usually moving in the normal seasonal directions and most headed to the appropriate side of downwind to bring their tracks closer to this direction (Griffin, 1972, 1973).

Most of the available field data refers to birds flying beneath cloud layers and to birds that initiated migration at some distance from the point of observation. Most of the birds that have been observed, therefore, may simply have been maintaining an orientation established many hours and kilometers earlier (cf. Emlen, 1975). This might be easily accomplished by reference to landmarks or wind direction (see below).

Data on the selection of flight direction under precisely known weather conditions are critical to an evaluation of the importance of stars or other visual cues. Emlen & Demong (1978) released White-throated Sparrows *(Zonotrichia albicollis)* carried aloft by balloon under solid overcast skies at night. While their orientation was not as accurate as birds

Department of Biological Sciences, State University of New York, Albany, New York, U. S. A.

released under clear skies and it took them longer to establish a consistent heading, 10 of 13 birds selected a meaningful migratory bearing. My own data on tracks under overcast are outlined in the following section.

Sun

Whereas the existence of a time-compensated sun compass in some birds has been known for decades, the role of the sun in migratory orientation, especially in nocturnal migrants, has been largely ignored. A few species of nocturnal migrants are known to possess a functional sun compass (von ST. PAUL, 1953; ABLE & DILLON 1977) and recent orientation cage experiments (MOORE, 1978; BINGMAN & ABLE, MS.) have confirmed KRAMER'S (1949) early suggestion that a view of the sun near sunset was important to subsequent nocturnal orientation.

Field data relevant to this hypothesis are few, but they constitute some of the most important recent findings from field studies of migratory orientation. In eastern New York I have radar tracked migrants under a variety of carefully documented environmental conditions. Appropriate seasonal migratory directions were observed when the birds could see stars or had seen the sun near sunset. When neither of these visual cues was available the birds oriented downwind even when this resulted in flight in seasonally inappropriate directions (ABLE, 1978, MS.). EMLEN & DEMONG (1978) released and tracked White-throated Sparrows (*Zonotrichia albicollis*) during early twilight when neither the sun nor stars were directly visible. The sparrows initiated well-oriented migratory flights, presumably based on the glow of sunset in the western sky. These results and others discussed below suggest that the sun plays a more important role in nocturnal migratory orientation than has been previously appreciated.

Wind direction

Wind affects migrants in three ways: 1) it may influence the probability that an individual will initiate migration on a given night, thereby giving rise to strong correlations between nightly migration magnitude and wind direction; 2) flying birds may be drifted by lateral wind components; 3) wind may be used as a directional cue.

In the inland southeastern United States both spring and fall passerine migrants virtually always orient downwind even when this results in flights in seasonally inappropriate directions (GAUTHREAUX & ABLE, 1970; ABLE, 1974a, b). This behavior does not generally occur among birds departing from Florida in autumn (WILLIAMS, et al., 1977) nor in the northeastern United States (DRURY & NISBET, 1964; NISBET & DRURY, 1967; RICHARDSON, 1971, 1972; ABLE, 1974b) or the Caribbean area (RICHARDSON, 1974, 1976).

Even in regions where passerine migrants do not always fly downwind, so-called reversed migrations are a regular occurrence (LOWERY & NEWMAN, 1955, 1966; DRURY & KEITH, 1962; DRURY & NISBET, 1964; NISBET & DRURY, 1967; RICHARDSON, 1971, 1972; ABLE, 1974b; 1978). In fact, these movements occur in many directions, not simply opposite the normal seasonal flow, and they may represent several quite different behaviors. Virtually all reported migrations in reversed or other inexplicable directions involved downwind flight. They sometimes involve substantial overwater flights (RICHARDSON, 1972) and although usually of smaller magnitude than "forward" migration, reversed migrations often include many thousands of birds.

In regions such as the northeastern United States where migration in the normal seasonal directions often occurs in headwinds, the factors associated with reversed and other inexplicable orientation need to be examined carefully. In eastern New York I have been using a short-range tracking radar during nine migration seasons. Forward migration often occurs at large angles to the wind or even into headwinds (ABLE, 1974b, 1978). Downwind flight in reversed or peculiar directions occurs almost exclusively under solid overcast skies that have also prevented the birds from seeing the sun late in the day (see above) (ABLE, 1978). COCHRAN et al. (1967) radio tracked four thrushes that initiated migration under overcast and in winds counter to the normal migration direction. These birds also migrated downwind.

A bird that does not orient directly with or into the wind will follow a track over the ground that is different from its air velocity. There has been much discussion in the literature concerning whether such birds are heading toward their presumed migratory goal and being drifted by the lateral wind component or are adjusting their air velocity such that their path over the ground (track) is constantly toward the goal. In fact, no unequivocal conclusion can be reached unless the goals of birds observed are actually known and this has virtually never been the case.

In the United States, DRURY & NISBET (1964), NISBET & DRURY (1967), BELLROSE & GRABER (1963), BELLROSE (1967) and RICHARDSON (1971, 1972) concluded that passerine nocturnal migrants corrected for drift while in flight. GAUTHREAUX (1972), ABLE (1974b) and WILLIAMS et al. (1972, 1977) obtained evidence of passive drift. Whereas all may be correct, the evidence is circumstantial and the conclusions based on assumptions about goal directions or their constancy from night to night.

Less ambiguous evidence of drift was obtained in birds descending through zones of changing winds (WILLIAMS et al., 1972), but the birds were flying between opaque cloud layers. EMLEN & DEMONG (1978) observed eastward tracks of White-throated Sparrows released from Wallops Island, Virginia. These birds were heading northward in strong cross winds and were certainly being drifted. Finally, the frequent occurrence of certain migrant species offshore from North America in both the Atlantic and Pacific Oceans (BAIRD & NISBET, 1960; RALPH, 1971; DESANTE, 1973; ABLE, 1977) and the long-range displacement of even fast-flying species (NISBET, 1959, 1963; BAGG, 1967) provide indirect evidence for the occurrence of wind drift.

Magnetic cues

There is very little direct evidence that the orientation direction of free-flying migrants is influenced by magnetic information. The only available data are slight and perhaps biologically insignificant counterclockwise changes in direction correlated with magnetic storm intensity (K-indices) (RICHARDSON, 1976; MOORE, 1977).

Landmarks

There is a strong general concensus that nocturnal migrants are usually not influenced by topographic features or other cues on the ground. The evidence usually consists of observations of migrants passing over coastlines, islands or other major landmarks without changing course. There are a few exceptions to this general pattern (LOWERY & NEWMAN, 1966; GAUTHREAUX, pers. comm.; RICHARDSON, MS.), and the behavior of night migrants

in response to major landmarks may depend on geographic locality or the motivation of the birds. Landmarks may well be important in subtler behavior (e.g. gauging wind drift), but data are few.

Orientation accuracy

Effects of overcast

The behavior of birds migrating under solid overcast skies provides a test of the importance of celestial cues in the maintenance of orientation. Virtually all surveillance radar and ceilometer data are consistent in showing that birds do not become disoriented under solid overcast (reviewed in Emlen, 1975), although the magnitude of migration is often reduced (see Richardson, 1978). The very rare instances of disorientation observed in the field have been associated with low overcast, fog or rain.

Even under very unfavorable conditions, individual birds seem able to maintain straight and level flight. Williams et al. (1972) and Griffin (1972, 1973) have obtained surprisingly straight and level tracks from birds flying between and within cloud layers. With a 10-cm tracking radar I have been able to obtain a few tracks of birds that initiated migration under solid, low overcast and were tracked as they flew through light rain. All have been as straight and level as migrants under optimal conditions.

Detailed tracking radar studies have recently revealed some subtle effects of overcast on the accuracy of orientation. I have compared the headings of passerines flying under solid overcast with those under clear skies. In general, there is greater variance among headings on overcast nights and occasionally the degree of orientation of the population of migrants aloft is greatly deteriorated. However, the individual birds comprising these flights yielded tracks as straight as those under clear skies and their headings were very consistent within tracks. The decrease in the accuracy of orientation under overcast was due, then, to variance in headings among birds.

A small, but growing, body of data suggests that overcast of several days' duration has more profound effects on orientation. Hebrard (1972) witnessed a large increase in the variance among tracks of fall migrants departing southern Louisiana following over 24 hrs. of solid overcast. Emlen & Demong (MS.) observed a drastic increase in the spread of flight directions of nocturnal migrants over Wallops Island, Virginia, during 8 days of nearly continuous overcast. A brief break in the clouds in the late afternoon of the fifth day was followed by an improvement in directionality. I observed a similar deterioration in orientation during 5 days of continuous overcast in September, 1977.

While the evidence is by no means conclusive, the data suggest that over the short run birds may rely on back-up directional cues (e.g., wind direction) or transfer information from one cue system to another. Over periods of two or more days without a view of either sun or stars, this ability seems to wane and the directions selected by the individual birds become increasingly dispersed, although each remains capable of maintaining straight and level flight.

Magnetic disturbances

Several studies failed to reveal any relationship between the degree of orientation of migrants and the intensity of natural magnetic storms (Able, 1974a; Richardson, 1974,

1976). However, the effect, if any, is likely to be very subtle and a large data set with a large number of high K values may be necessary to detect it above other variability. The only report of a positive correlation between spread in flight directions and magnetic disturbance is MOORE's (1977) analysis of ceilometer data from the southeastern United States. LARKIN & SUTHERLAND (1977) tracked nocturnal migrants passing over the underground antenna of Project Seafarer (Wisconsin), and found that birds were more likely to turn or change altitude when its A-C field was being turned on or off.

Discussion

If the field data on migratory orientation in North America show anything, it is that the behavior is complex and variable. Depending upon where they are in the migratory journey, birds respond differently to directional cues. In the inland southeastern United States passerines rely on wind direction to the exclusion of other available information. At higher latitudes, where general wind patterns are less favourable, downwind flight in other than the normal migration direction is rare and seems to occur primarily when the birds are unable to see sun or stars. The widely varying data on wind drift may also be partly explicable in the same way. Individuals of species not adapted to make long overwater flights must avoid being drifted a offshore, e.g., from New England. We might expect these birds, which normally move southwestward parallel to the coast, to correct for lateral drift when in coastal areas and this behavior might be facilitated by the use of coastal landmarks. At other points along the route or in other regions, drift poses no threat and it may be more efficient to undergo some displacement. Indeed, WILLIAMS & WILLIAMS (1978) have shown that the trans-Atlantic flights of passerines may be possible only because the birds maintain a constant southeast heading, taking advantage of easterly trade winds to drift them toward the South American continent. Although there is no evidence that migrants employ goal-directed navigation during all phases of their migration, the evolution of these spatially varying flight strategies requires that the birds assess at least general information about their location.

A somewhat greater degree of sophistication may be involved in cases where migrants reorient to compensate for displacements or flight over the ocean. In coastal situations this behavior is of regular occurrence (e.g., BAIRD & NISBET, 1960; DESANTE, 1973; RICHARDSON, MS.) and is of obvious adaptive value. Recent observations in the southeastern United States (GAUTHREAUX, 1978) suggest that the same phenomenon may occur inland although the adaptive significance is much less obvious. It is perhaps consistent that morning reorientation seems not to occur far inland in the northeastern states where birds appear to be subjected to wind displacement much less frequently. These behaviors can also be explained without invoking navigation (EMLEN, 1975; ABLE, 1977).

Perhaps the greatest shortcoming of nearly all field studies, especially studies of nocturnal migration and those employing radar, is that species and age classes cannot be discriminated. However, a few major differences in behavior have been documented: e.g., the flight directions of shorebirds and waterfowl are less influenced by wind direction than those of passerines (ABLE, 1974a); some species regularly make a trans-Atlantic crossing to South America in autumn whereas others migrate coastwise (NISBET, 1970; RICHARDSON, 1974, 1976; WILLIAMS & WILLIAMS, 1978). Orientation behavior is also known to require

experience for proper development (see WILTSCHKO's review in this volume). If our data could be sorted in the basis of species and age, much variability might be explained. At present these problems seem approachable only by carefully combining experimental and observational techniques.

The data from field studies in North America indicate that migratory orientation is a complex, highly sophisticated behavior. There is considerable support for the idea that migrants are equipped with several back-up compass systems and recently some clues have been obtained as to how these cues relate to one another. For many years there have been tantalizing suggestions that migrants employ non-visual orientation mechanisms. However, to date there is no field evidence directly suggesting what they might be. Magnetic orientation has been shown under controlled conditions, but there is no evidence that migrants use magnetic cues during flight, although proper and sufficient attempts to find such effects have not been made.

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Radar Data on the Orientation of Migratory Birds in Europe

Bruno Bruderer

Introduction

North American migrants seem to follow the large-scale average wind pattern in extensive loop migrations (cf. Gauthreaux 1979). In Europe, however, the complicated distribution of land, water and mountain areas, the course of the winter isotherms (favouring perpendicular paths of migration), the rapid eastward movement of cyclones with the temperate westerlies, and local effects (as leading-lines and local winds) lead to a much more complex migratory system.

Radar evidence on migratory orientation was reviewed by Lack (1962). The present paper summarizes new evidence and ideas arising from radar observations in Europe, with special emphasis on passerine migration. In order to reduce the number of references, I omit publications prior to Lack's review and refer to Eastwood's (1967) "Radar Ornithology" for all papers cited therein (by the indication "in e"). I limit my list of references to subsequent publications without attempting a complete review.

Directional pattern of migration in Europe

Lack (l.c.) mentioned five cases of large scale directional changes in the European-African bird migration system (Norwegian *Fringilla coelebs, Calidris canutus* immigration to Britain, British long-distance migrants across the Channel, and winter guests to tropical Africa needing to change direction in the western or eastern Mediterranean, respectively). He suggested that these shifts in standard direction might be released according to an innate program after a given time or distance flown, or when the birds reach a given latitude.

The additional radar information, very coarsely summarized in Fig. 1, combined with ringing results, indicate that directional changes might be a common feature of migration throughout Europe:

a) Passerine night migrants leaving Norway with following winds reach the British Islands with directions around SW/SSW; when drifted by easterly to southerly winds they arrive on a WSW or even W course. Departures from eastern Scotland and northeastern England suggested that at least part of these migrants redetermine their migration later towards directions around SSE (Myres 1964 in e, Wilcock 1965 in e, Evans 1966 in e). They are joined by migrants from Iceland (first on a SE course) and Greenland (initially on a ESE course) (Lee 1963 in e), and by the British summer residents, leaving Britain largely on a SSE/SE course, later turning SW on the Continent (Lack & Eastwood 1962 in e). In contrast to the early autumn emigration the proportion of late spring immigration from the SSE is small, indicating that (experienced?) migrants tend to minimize detours in spring or close to their goal areas (cf. tables in Lack 1963 in e).

b) In southern Sweden (Alerstam 1972, Alerstam & Ulfstrand 1972, 1975, Alerstam 1975, 1976) and in eastern Denmark (Rabøl et al. 1971, 1972) a strong and very

Schweizerische Vogelwarte, CH-6204 Sempach, Switzerland

frequent SE/SSE night emigration (with a large porportion of thrushes) takes place in autumn. Even more pronounced than in England, these SSE movements fail to find an equivalent in spring, and they seem to be too large to be explained by Scandinavian summer residents wintering to the SE. This suggests that additional populations from E of the Baltic, and Scandinavian birds with winterquarters to the S/SW may be involved.

c) In spring and autumn the main stream of migrants along the Swiss Alps deviates by about 30° from the directions of comparable ringing recoveries, suggesting a preference for flights parallel to the Alps, possibly as an evolutionary adaptation to the prevailing winds in this area (Bruderer 1978).

d) In the Mediterranean a migratory divide is indicated at similar longitude as documented by ringing recoveries for northern Europe, and slight hints to changes in directions at the W coast of Iberia are available (Casement 1966 in e). However, according to Houghton (1970) the directions at Gibraltar depend to a high degree on actual winds.



Figure 1. The main directions of autumn migration are indicated by arrows (according to publications mentioned in the text). Dashed lines indicate assumed flight paths (according to ringing results). The dash-point line is the winter isotherm of 0° (bent northward in western Europe by the warming effect of the Gulf Stream). The topographical complexity of the Continent is emphasized by the main ranges of the Cenozoic orogenic belt.

Winddrift and preference for following winds

The best and apparently most often used means to avoid involuntary deviations by drift is to reduce migratory activity in unfavourable winds. Furthermore, there is good evidence that birds migrating in undisturbed weather are concentrated at levels with most favorable winds (Bruderer 1971, Bruderer & Steidinger 1972). During nights with different wind directions at different levels, birds select altitudes with winds closest to their tracks (Steidinger 1972, Bruderer 1975). Tracking of single migrants on nights with unfavour-

able winds showed that most of the few birds aloft were climbing or descending (what could be interpreted as search for more favorable conditions; Bruderer in prep.). A third possibility is partial compensation for wind speed (Bruderer 1971).

Cases where preferred tracks and wind direction coincide exactly are rare, and the question arises whether the birds tend to compensate for this lateral displacement a) within the main part of the flight, b) towards the end of it, c) on a subsequent take-off, or d) not at all.

Alerstam (1976b) recalculated the published data on drift effects and concluded that all the reported cases of drift over land can to a large extent be explained by pseudodrift (i.e. migration of different populations when winds are favourable for them; cf. also Evans 1966 in E, Lack 1969). Real drift (partial or complete) had to be assumed over sea (cf. the North Sea movements cited above, e.g. Parslow 1969). Alerstam & Petterson (1977) demonstrated that the amount of drift in *Grus grus*, *Columba palumbus*, and *Turdus iliacus* over the sea corresponded to what was to be predicted if the birds were drifted according to the motion of the waves. Tinbergen's (1956 in E) hypothesis that birds may continuously project their intended track direction to a reference system on the Earth, obtained new support from this observation.

Evans (1966 in E) and Steidinger (1972) gave evidence that birds compensate to a high degree for side wind components of a following wind, while side wind components of opposed winds cause directional changes. In my (Bruderer 1975, 1977, 1978) papers I confirmed the birds' capability for compensation of drift towards inappropriate directions. On the other hand I emphasized that combined effects of pseudodrift, compensatory movements, leading-lines, incomplete compensation, and down-wind flights (including reversed migration) may be an explanation for the large scatter of directions over inland areas at low levels.

Rabøl (1974) as well as Alerstam & Ulfstrand (1975) reported a small amount of real drift for high flying day migrants over land, and overcompensation of the wind at low levels. As suggested by Rabøl (l.c.) it might often be more profitable to accept a certain (though small) drift when flying at high altitudes, and to make use of the low wind speeds close to the ground to compensate (over a short distance, towards the end of a journey) for the previous drift.

Landmarks and leading-lines

Surveillance radars have supported the view that the main mass of diurnal and especially of nocturnal migrants usually cross a coastline without any deviation (Lack 1962, Eastwood 1967). This statement can still be accepted for most of the large high altitude movements in favourable winds, which probably cover the main part of the birds' journey. It is less true for arrivals after a long sea crossing (Buurma, in discussion) and for movements at low levels (e.g. in adverse conditions, or towards the end of a journey), which are often underestimated by surveillance radars.

A guiding effect with respect to the goals of migration is only probable in case of large topographical features, supposed to be involved in the evolution of preferred directions, and actually triggering or correcting inherited directional tendencies. Most of the leading-lines concentrating visible migration seem to have rather a deviating than a guiding effect; they seem to interfere with the normal orientational mechanisms instead of

supporting them. However, the size of such deviated movements is not negligible (cf. Bruderer & Winkler 1976). Autumn migrants tolerate important deviations in order to avoid unfavourable flight conditions, drift over sea, or inhospitable areas, indicating that not every deviation from a straight course between starting point and goal area is disadvantageous. Flights parallel to single ridges in the Alps (deviating from the previous direction or from the direction after leaving the line) may be a further indication of the continuous use of landmarks for the maintenance of tracks close to the preferred direction (cf. Bruderer, 1978).

Reorientation, redetermined movements, and reversed migration

Evidence for short-term in-flight reorientation is included in the observations of directional changes after leaving a leading-line in the Alps (Bruderer 1978) and in Rabøl's (1974) model on drift compensation.

Long-term changes of the preferred directions within single stages of migration seem to occur in Scandinavian *Fringilla coelebs,* whose tracks shift along a gradient running from WNW to ESE in accordance with Perdeck's (1970) model of the changing standard direction (Alerstam & Ulfstrand 1975). A similar shift in the preferred direction was observed for *Columba palumbus* in western Sweden (Alerstam & Ulfstrand 1973). In-flight reorientation of British emigrants on the Continent (cf. section 2) has been postulated (Evans 1966 in e), but up to now has never been seen on radar; redetermined departures can not be positively identified, because they mingle with the main SW movements on the Continent.

A special case of reorientation is known for autumn migration of Scandinavian thrushes towards the British Islands (Lack 1962, Lee 1963 in e, Myres 1964 in e, Wilcock 1964 in e). It was shown that thrushes finding themselves over the ocean at dawn, climb to higher altitudes and change direction towards SE. On the average this brings the birds which are out of sight of land back to land in the minimum time.

The main factor inducing real reversed migration (apart from simple hardweather movements) is wind against the normal direction of migration; reversed migration generally occurs at low levels. In our own observations (Bruderer 1978) it was more pronounced under cloudy sky, when the spread of directions is generally increased. Whether these reversed movements might be compensatory or have another meaning is still obscure.

Use of celestial cues, diurnal changes in direction, and reduced visibility

There is general agreement that migratory activity is somewhat reduced in the presence of frontal clouds and minimal in rain, and that the scatter in directions is largest in rain. There is evidence that birds avoid staying within clouds. Whenever possible they fly around a cloud bank, they stay below a cloud layer or climb above it. Released inside clouds they seem to circle around until they see a gap below or above them and dive or climb towards this gap (Bruderer 1977).

Steidinger (1968) showed increasing scatter of directions for birds departing below high stratus layers lasting for several nights. The two cases of randomly scattered directions of diurnal migrants reported by Gehring (1963 in e) similarly refer to

situations where the two previous days had complete overcast. Both authors reported that the tracks of the birds below the stratus were straight and that the birds flying above the cloud cover showed minimal scatter of directions.

In undisturbed weather the mean direction of migration in the Swiss lowlands shows usually a clockwise shift on the order of 10 to 20° during the night. It shifts back at beginning of day migration, reaches again maximum deviation at noon and returns to the starting direction during afternoon (cf. Gehring 1963 in e, Steidinger 1968, Bruderer 1975). Gehring (l.c.) suggested that the diurnal shift could be explained by the birds' inaccurate compensation for the sun's movement. An explanation for the nocturnal shift is still lacking, although some sort of incomplete compensation of the clockwise movement of the stars in front of spring and autumn migrants seems possible.

A remarkable indication of the use of celestial cues has been described by Lee (1963 in e), who assumed that a departure from the Outer Hebrides deviating by 130° from normal was due to the birds' taking the rising moon for the setting sun.

Discussion and results

The constant presence of localized directional changes of migratory paths in spite of varying conditions seems to imply an innate component. The number and the relatively small scale of such directional changes, however, leads to the assumption of superimposed external triggering or correcting factors, which probably have been involved in the evolution of the actual pattern.

Available evidence suggests that European migrants have evolved migratory paths and selective behaviour which allow them to make use of the most frequent winds in the departure areas and to reduce crossing of inhospitable areas. In spring deviations and selectivity for favorable winds seem to be reduced (except before an extensive sea crossing, e.g. at the Outer Hebrides).

We assume that the selectivity for favorable wind directions decreases a) with the lowering of the threshold for migration (i.e. with increasing migratory urge), b) with the shortening of the distance to fly, c) with the higher speed capacity of the species involved, and d) with increasing experience (i.e. with increasing correcting ability) of the individuals involved.

Birds are able to compensate for drift over land. Drifting of migrants over the sea according to the motion of the waves, as well as some leading-line effects indicate that the use of reference systems on the ground is an important means for drift compensation and maintenance of selected tracks. However, it seems that drift compensation is not always used to its full extent: tolerating partial drift at high altitudes and overcompensation at low levels (in low wind speeds) seems to be a better strategy. Leading-lines concentrate, facilitate, and possibly often induce compensatory (or evasive) movements below the optimal altitude range of most radars. On the other hand the high-level main movements which usually seem unaffected by leading-lines are most conspicuous for surveillance radars. Some cases of in-flight reorientation have been reported, while there is only circumstantial evidence for redetermined departures. Reversed migration as well as other deviations from normal directions are most pronounced under adverse winds and cloudy sky. Full overcast throughout several days leads to increasing scatter of directions in day

and night migration, while the tracks remain straight. Clockwise shifts of directions during day and night need further study.

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Decision Making by Nocturnal Bird Migrants: The Integration of Multiple Cues

STEPHEN T. EMLEN

Most investigators agree that migratory birds do not rely upon a single navigational cue when selecting a flight direction, but rather on a complex array of multiple, and often redundant, directional information (see KEETON, 1974; EMLEN, 1975). This realization leads one to ask new questions: How are these different directional inputs integrated with one another? Is there a hierarchy of importance of different cues, and does this change with the age or experience of the bird, the meteorological or magnetic conditions during flight, or the geographic position of the traveling bird?

In this paper I a) suggest that the quiescent period immediately preceding nocturnal migratory departures is a critical time for the integration of directional information, b) review some of the evidence that migrants integrate and calibrate different cue systems as they select a direction for flight, and c) discuss recent work in which the relative importance of different cue systems was analyzed by releasing and tracking birds as they initiated flights under controlled conditions.

The importance of the Einschlafpause

Nocturnal songbird migrants typically remain inactive during the late transition period between daylight and darkness. This "Einschlafpause" (PALMGREN, 1949) has been universally reported, whether from studies of caged activity of migrants, by direct visual observations of migratory departures, or from surveillance radar studies that show waves of departures occurring 30 to 45 minutes after the beginning of civil twilight (PALMGREN, ibid.; RIKER, 1977; HEBRARD, 1971; GAUTHREAUX, 1971; RICHARDSON, 1970). Certain directional cues become unavailable after dark; others assume importance at this time. I suggest that this quiescent period is one of great importance for the individual migrant. Not only must it make the decision of whether or not to initiate a migratory flight that night, but it must also select its migratory direction. It is probably at this time, while on the ground prior to departure, that the bird integrates and calibrates the various types of directional information at its disposal. If the sky is clear, these might include the late afternoon position of the sun, sunset itself, and the early evening locations of star patterns. Geomagnetic information can also be incorporated, as might be meteorological input concerning the direction of the winds aloft. Topographic features in the immediate surrounding of the bird should serve as temporary reference points. In this way, even if critical information becames obscured or is lacking at the exact time of departure, the bird could still select its migratory bearing by referring to the topographic features nearby that had taken on directional significance.

The calibration of different cue systems

Recent studies suggest that one advantage of the availability of multiple cues is to allow

Section of Neurobiology and Behavior, Division of Biological Sciences, Cornell University, Ithaca, New York U.S.A.

for a cross-checking or calibration of one system against another. This idea is not new; it was understood by VLEUGEL (1954) who was one of the first to propose a calibration system between multiple cues. VLEUGEL also realized the important distinction between the selection and the maintenance of a migratory direction. The selection process presumably requires more information and probably relies more heavily upon integration of different inputs than does the maintenance of that direction once the bird is aloft. According to VLEUGEL's model, sunset provided the primary reference for the selection of a departure bearing. Once in flight, the bird integrated information from a secondary reference cue, the direction of the winds aloft. After the glow of sunset had faded, the night migrants could continue on course in the absence of the primary cue by maintaining the same, constant, angle relative to the wind.

Recent experimental evidence is beginning to suggest a series of additional calibration systems.

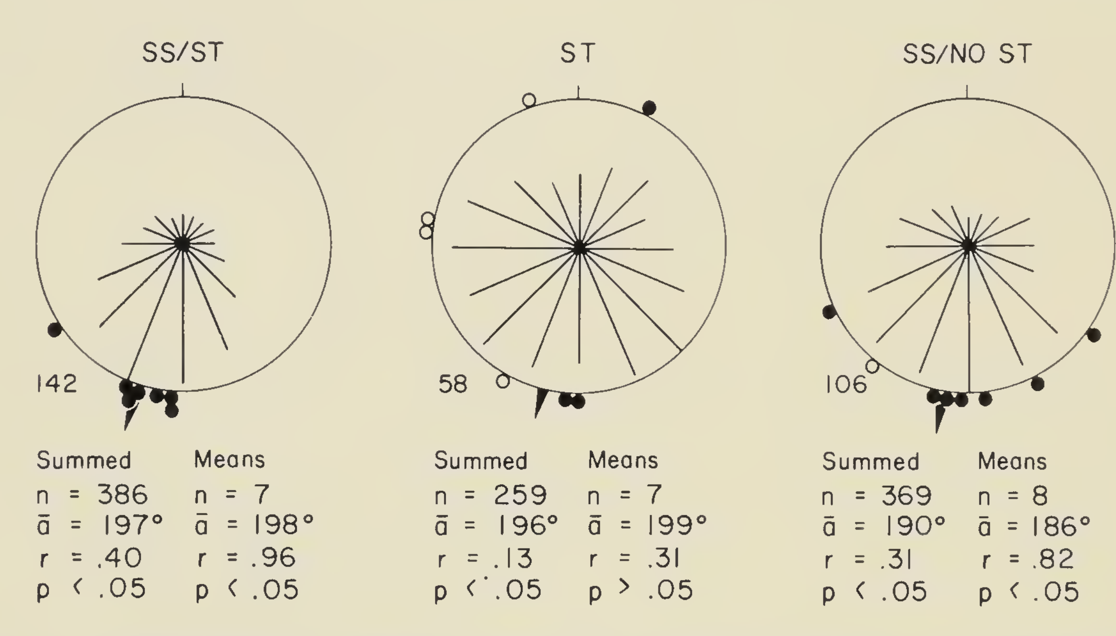


FIGURE 1. A comparison of fall orientation behavior of caged Savannah Sparrows allowed to see the sun plus stars (left), stars only (center), and sunset only (right). Vector diagrams represent the summed activity for a given test situation and are drawn such that the radius equals the greatest number of activity units in any one $22^1/_2$ deg. sector (lower left of each circle). The arrow on the circumference gives the mean direction of the summed activity. The dots on the circumference represent the mean headings of the individual birdnights where a black dot indicates a statistically significant ($p<.05$) heading and a white dot nonsignificant ($p>.05$). Statistics are presented for both summed and means procedures: $\bar{a}$ = mean direction of activity or headings, and r= length of mean vector and is a measure of the concentration of activity or headings. North= 360° and is to the top of the figure.

It has long been known that many species of nocturnal migrants will accurately display an appropriate migration bearing in an orientation cage when placed outdoors under the natural night sky or under the artificial heavens of a planetarium (for review see EMLEN, 1975). What has gone unreported is that several species show poor or inconsistent orientation when tested under similar conditions. F. MOORE has conducted a series of experiments to investigate the potential importance of viewing the late afternoon sun and sunset for accurate stellar orientation in one such species, the Savannah Sparrow *(Passerculus sandwichensis)* (MOORE, in press). As "controls", sparrows were placed in circular orientation cages at sunset, and exposed to both twilight and night sky conditions.

As "experimentals", the same birds are tested under starry skies, but without prior exposure to sunset. MOORE finds that during both spring and autumn migration seasons, the control birds show marked improvement in both the consistency and accuracy with which they take up appropriate migration directions (see Figure 1). He concludes that stellar cues take on a directional meaning or significance to the Savannah Sparrows as a result of a transferral or calibration of information provided by the setting sun.

Somewhat analogous experiments, but involving different cue systems, have been performed by W. and R. WILTSCHKO, 1975a, b). Using several species of European warblers (especially *Sylvia borin*) and the European Robin *(Erithacus rubecula)*, they tested migratory orientation in outdoor cages when directional information from the stars and from the magnetic field was in conflict. Octagonal orientation cages were set up outdoors in Spain. A large pair of Helmholtz coils surrounding each cage allowed the direction of the magnetic field to be altered, and a screen blocking direct view of the coils permitted a direct view of 95° of the sky overhead. (It is unfortunate that this area could not be larger, since the circumpolar stars that have been shown to be of critical importance for stellar orientation in the Indigo Bunting were not available to the birds in these experiments). In autumn experiments with *Sylvia borin*, the birds took up appropriate migratory directions when the magnetic and stellar cues were coincident, but shifted their direction in accordance with the artificial magnetic field when it was deflected 120° (see Figure 2). Interestingly, the birds continued to orient in the shifted direction after magnetic information was eliminated (by canceling the horizontal component of the earth's magnetic field). From these experiments, the WILTSCHKOS concluded that the migrants were transferring information from the geomagnetic compass to the stars in the night sky.

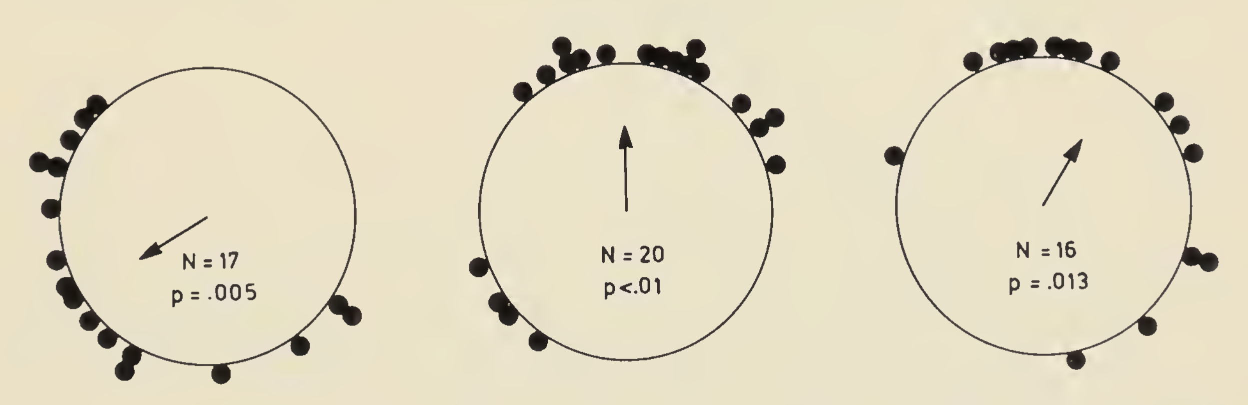


FIGURE 2. Orientation of European warblers tested under the natural night sky in Spain when magnetic cues coincide with (left), conflict with (center) and are eliminated from (right column) coincidence with stellar information. Each dot represents the mean direction of one bird on one night of testing. The arrow is the mean vector for the sample; its direction is the mean direction and its length is a measure of the consistency of orientation (r). The sample size (N) and the significance of the orientation by RALEIGH tests (p) are given in the center of each circle. Data redrawn from WILTSCHKO & WILTSCHKO, 1975a.

Similar results were obtained with European Robins during the spring migration season, with the difference that the birds continued to orient by the stellar cues for a period of three to nine days after the magnetic field had been altered before shifting their direction to correspond to the new magnetically appropriate direction. It appeared that the stars were taking on meaning or being calibrated against the magnetic compass, with this calibration taking place frequently with *Sylvia borin*, but less regularly with *Erithacus rubecula*.

Many years ago, during studies of the ontogenetic development of orientation capabilities in Indigo Buntings *(Passerina cyanea),* I hypothesized that individual stars and patterns of stars were of no value for direction finding until their position with respect to some reference framework had been learned (Emlen, 1970, 1972). Since adult Indigo Buntings (unlike Savannah Sparrows) can use stellar information without the need for integration with sunset, I performed a series of ontogenetic experiments in which early exposure to celestial information was controlled. One group of young birds never saw the night sky until their orientational capabilities were tested during their first autumn migration season. A second group was allowed regular exposure to a normally rotating, seasonally appropriate, planetarium sky. And a third group was given equal exposure to a rotating planetarium sky, with the sole difference being that the axis of rotation was shifted roughly 90° (relative to geographic and magnetic north) and rotated around the star Betelgeuse rather than Polaris. The results, shown in Figure 3, document a) the extreme importance of early experience and learning for the development of star orientation capabilities, and b) the importance of the axis of rotation in providing a directional reference against which patterns of stars take on directional meaning.

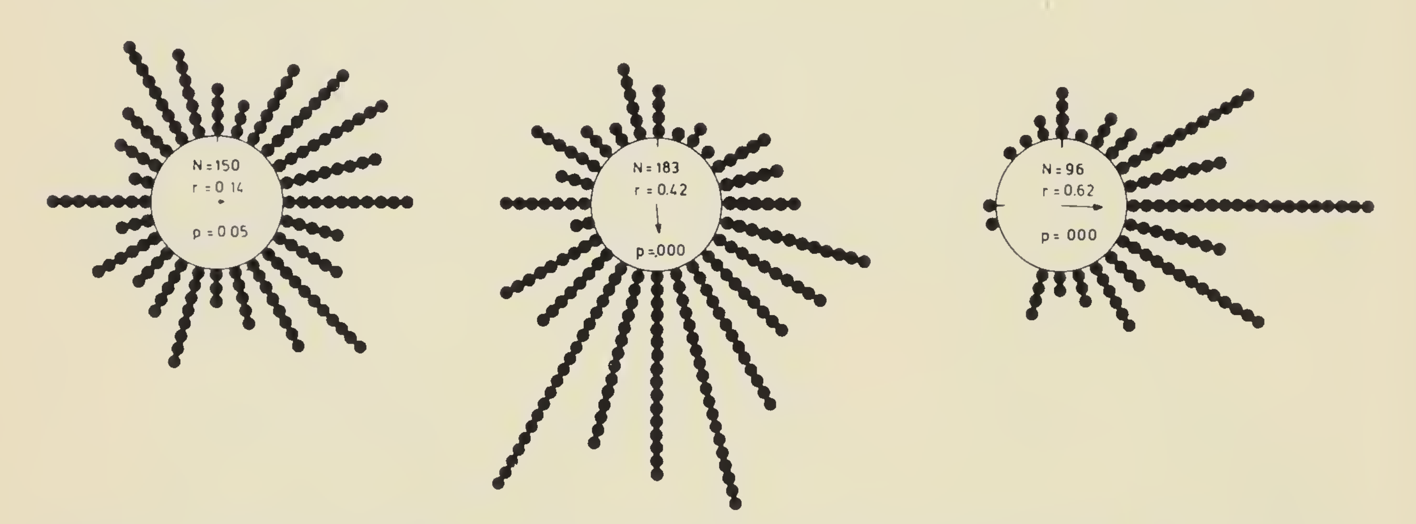


Figure 3. Migratory orientation of three groups of young Indigo Buntings, reared under the following conditions. Left: No exposure to stellar cues prior to being tested during their first automn migration season. Center: Frequent exposure to a seasonally appropriate planetarium sky rotating about the normal north–south axis (Polaris equals the pole star). Right: Frequent exposure to the same planetarium sky but with the axis of rotation shifted 90° such that Betelgeuse becomes the new "pole" star. All diagrams are drawn with magnetic north= 310°. Notation is the same as in Figure 2. Data redrawn from Emlen, 1972.

These three studies show that a series of different cues (the setting sun, the earth's magnetic field, and the axis of rotation on the night sky) can all be used by different species of birds as part of the process whereby stellar cues take on directional meaning and are integrated into the nocturnal orientation system. It is still too soon to speculate on whether additional calibration systems will be discovered, or to understand the adaptive reasons why different species seem to have different strategies of integration and calibration.

The relative importance of different directional cues

N. J. Demong and I recently completed a study of the relative weighting of different orientational cues by migratory White-throated Sparrows *(Zonotrichia albicollis).* We used

the technique of capturing individual sparrows, exposing them to various experimental manipulations, and then rereleasing them at migratory altitudes and allowing them to initiate migratory flights while being followed by a tracking radar. In an actual experiment, a sparrow was placed in an especially designed cardboard box equipped with a fuse-operated opening device (DEMONG and EMLEN, in press). This box was attached to a helium-filled weather balloon which carried the bird to the desired altitude. The fuse then allowed the door of the box to swing open, thereby releasing the bird. Through the cooperation of the National Aeronautics and Space Administration, each bird was tracked by a FPS-16 tracking radar as it made its decision, selected a direction, and initiated the first 8 to 20 kilometers of a migratory flight. In this way we were able to assess the relative importance of celestial, magnetic, meteorological (wind) and topographic cues.

When released under clear night skies, the sparrows rapidly selected departure bearings to the north-northeast. Tracks were straight and exhibited a mean direction of 18° (see Figure 4). This corresponds well with the expected direction of spring migration for White-throated Sparrows, independently calculated from banding recoveries to be 31°.

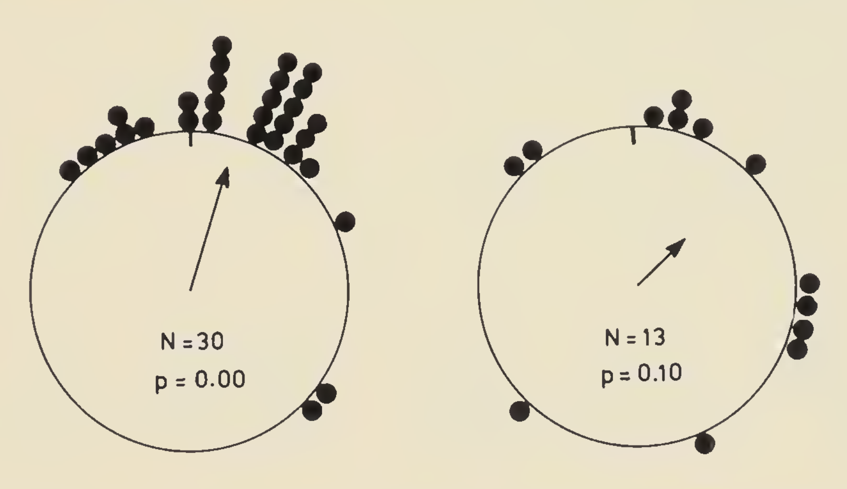


FIGURE 4. Departure directions of individual White-throated Sparrows released under clear (left) and overcast (right) skies and tracked by NASA FPS–16 tracking radar. Notation is similar to that described in Figure 2.

Sparrows released under total overcast showed several differences in behavior when compared to those released under clear, starry skies. Many hovered or circled for several minutes after release before actively initiating a flight. Even after adoption of a flight direction, marked sinusoidal deviations from a straight track were common, and airspeed was low. Further, there was a marked deterioration in orientation ability, although the mean direction of the departure tracks was still to the northeast (Figure 4). In summary, it would appear that many birds released under total overcast were able to determine a northerly direction, but that the process took longer and was less accurate than when selected under clear skies.

These results are especially interesting since numerous surveillance radar studies have provided convincing evidence that nocturnal migration continues and that most migrants are well-oriented on overcast nights when stellar cues are totally obscured. In fact, our own surveillance radar data showed that birds departing of their own volition were well-oriented to the northeast on many of the same nights when our artificially released birds were showing poor orientation. We believe that this discrepancy is consistent with

the distinction between selection and maintenance of migratory directions. The birds observed on surveillance radar had had the opportunity of remaining on the ground during the twilight period and integrating various sources of directional information at their disposal. The artificially released birds had no opportunity for such leisurely integration and were totally deprived of the use of sunset or local topographic reference markers as directional cues.

This point was further emphasized by a "natural experiment" that occurred during mid-May of 1972 when a low pressure cell became stationary near the Atlantic coast causing a prolonged period of continuously total overcast weather that extended uninterruptedly for eight days. Figure 5 (from EMLEN & DEMONG, in preparation) shows the orientation of naturally occurring migrants as measured by the NASA surveillance radar on these dates. In all cases when the position of the sun and sunset had been obscured for periods of one day or longer, serious disorientation occurred among the migrants aloft (note that all celestial cues, sun, sunset and stars, were unavailable during this period). These types of results suggest a strong importance of celestial information in the selection of the migratory direction.

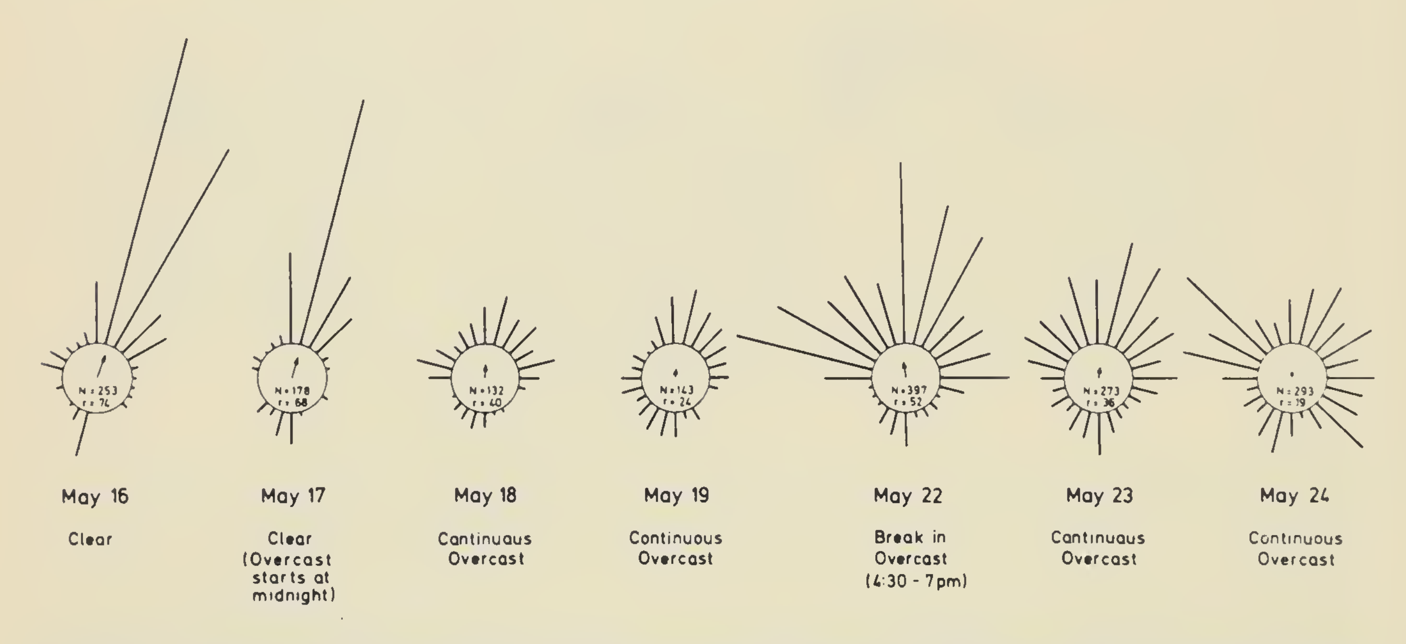


FIGURE 5. Orientation of naturally occurring migrants passing over Wallops Island, Virginia during a prolonged period of continuous overcast (and observed by ASR–7 surveillance radar). 0° represents geographic north, and each arrow is the mean vector for that night. Sample size (N) and the length of the mean vector (r) are given in the center of each diagram.

We have little information pertaining to the importance of magnetic information to the White-throated Sparrow. Five sparrows were released aloft under clear night skies with miniature ceramic magnets attached to their bodies. These birds showed no marked difference in orientation behavior from controls, but the critical experiments of releasing such birds under total overcast conditions were not performed.

GAUTHREAUX and ABLE (1970) have suggested that winds aloft are another important orienting cue for migrants, at least in the southeastern portion of the United States. The importance of wind information was tested by releasing sparrows under a variety of favorable and unfavorable wind conditions. The migration direction selected showed no consistent tendency with regard to the direction of the wind. Some birds were released on

nights when the strength of the winds aloft was greater than the average airspeed of White-throated Sparrows. Under these conditions the birds were unable to control their tracks over the ground. But, interestingly, even under these "extreme" conditions, the sparrows adopted northerly *headings* that were indistinguishable from those taken on calmer nights. Thus the birds did not exhibit a tendency to fly downwind, but rather adopted northerly directions regardless of the strength or direction of the winds encountered aloft. Even under conditions of total overcast, the sparrows showed weak tendencies to the north and failed to shift to a downwind orientation. Thus it appears that wind cues, while undoubtedly of critical importance in the decision of whether or not to initiate a flight on a given night, did not play a key role in the selection of the migratory direction.

The location of the NASA tracking station where these experiments were conducted is on the coast of Virginia. Visual features of the landscape might thus provide strong orientational cues for migrants. To investigate this possibility, flight paths of the sparrows were overlaid onto accurate maps of the topographic landscape. Perhaps surprisingly, the sparrows showed little tendency to alter their courses in any manner that would bring them closer to, or more parallel with, the coastline. This was especially impressive in the tracks of the birds released under total overcast. With visual information from the sky obscured, one might expect visual cues from the ground to assume greater importance. Yet there was no tendency for these overcast tracks to converge along the coast. Many birds were slowly heading out to sea while others were traveling in various directions over the mainland. This is all the more remarkable considering the behavioral differences shown by the overcast birds (discussed above), all of which seem indicative of a greater difficult in selecting a direction, a lower motivation to migrate, or both. We conclude that even when flying under the potentially difficult orientational conditions imposed by total overcast, the birds were largely ignoring the dominant visual cues from the coastline below.

These results are consistent with a model that celestial cues (both sunset and stars) are of strong importance to migratory White-throated Sparrows; that sufficient alternate information is available for the selection of the correct migratory direction in their absence; that wind direction plays only a secondary role in migratory orientation; and that visual features of the ground below are near the bottom of any orientational hierarchy for this species.

Hopefully, this short review has illustrated the change in emphasis that is occurring in many orientational studies. Rather than searching for the mechanism of orientation, many researchers are now focusing on the relative importance of, the integration of, and the calibration between, different directional inputs as they function in the dynamic system of multiple cue orientation that typifies bird migration.

Acknowledgements

I would like to thank NASA, Wallops Island, and its director, R. Kreiger, for their tremendous cooperation with the tracking studies. N. J. Demong, W. Wiltschko and R. Wiltschko provided constructive criticism and F. Moore allowed use of his unpublished data. Financial assistance from the National Science Foundation (Grant Nos. GB–35199X and BMS 75–18905) is also gratefully acknowledged.

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The Relative Importance and Integration of Different Directional Cues During Ontogeny.

WOLFGANG WILTSCHKO

Introduction

In numerous bird species, the individuals migrate singly, and the young birds are able to reach their wintering area without the help of experienced conspecifics. Many experiments indicate that these young birds possess innate information about the distance (GWINNER 1968) and direction of their migration (PERDECK 1958; see EMLEN 1975). Yet innate directional information – like "south" – requires an external reference system to enable the bird to find this given direction, i.e. to determine where "south" lies. A literature review (e.g. EMLEN 1975) convincingly demonstrates that migratory birds use a variety of cues or cue systems for orientation, and thus the question arises which of these cues serves as a reference system for the genetically encoded migratory direction. Since natural selection would favour least expenses, and normally innate information is as scarce as is possible to master the pertaining situation (frequently to be later supplemented by learned information), it appears highly unlikely that the migratory direction is encoded relative to all possible orientation cues. Instead we might expect a calibration system where information from a primary reference is secondarily transferred to the other systems.

Here I will try to review three experiments that may help to answer this question, namely studies in which young birds were handraised with only limited access to the possible orientation cues, and their spontaneous directional tendencies were recorded in the following migratory seasons.

Night-migrating birds

SAUER (1957) was the first to test handraised *Sylvia* Warblers in a planetarium that had been isolated from all celestial cues. He concluded from his results that they possess an innate knowledge of the starry sky and its variability in time and geographic location. His findings, however, could not be confirmed by later investigators (EMLEN 1972, WILTSCHKO & WILTSCHKO 1975 a).

EMLEN (1972) handraised three groups of Indigo Buntings, *Passerina cyanea*. The first group never saw the sun or stars prior to the critical tests. Between the fledging age and the beginning of the migratory season, the other two groups saw a planetarium sky three nights per week. For the second group, the sky duplicated the natural situation in star patterns and rotation; for the third group, the axis of rotation was shifted away from the north star Polaris to Betelgeuse in the configuration of Orion. In autumn, all three groups were tested under a fixed planetarium sky; their pooled directional preferences are given in Fig. 1. The birds of the first group were not oriented (Fig. 1a). The birds of the second group showed headings lying "south" of Polaris (Fig. 1b), while the headings of the third group (being recorded during three nightly registration periods, where Polaris and Betelgeuse were shifted relative to each other between the periods) showed a large scatter

Fachbereich Biologie der Universität, Zoologie, AK P.Ö.V., Siesmayerstraße 70, D 6000 Frankfurt a.M., Bundesrepublik Deutschland.

with respect to Polaris (Fig. 1c, open symbols), but a clear orientation to the "south" of Betelgeuse (Fig. 1c, solid symbols). Thus both groups showed distinct directional tendencies under the fixed planetarium sky, the directions of which were found to be the expected migratory direction with respect to the axis of rotation they had experienced prior to the tests.

These data clearly demonstrate that in the Indigo Bunting the directional significance of the stars is not innate, but has to be established by experience. EMLEN concluded that one reference system of the migratory direction underlying this learning process is celestial rotation: in the period prior to their first migration the birds learn the position of the stars relative to the axis of rotation, and later they are able to find their migratory direction by the star patterns alone. The learning process is assumed to be happening once and to be effective for a long time (EMLEN 1972).

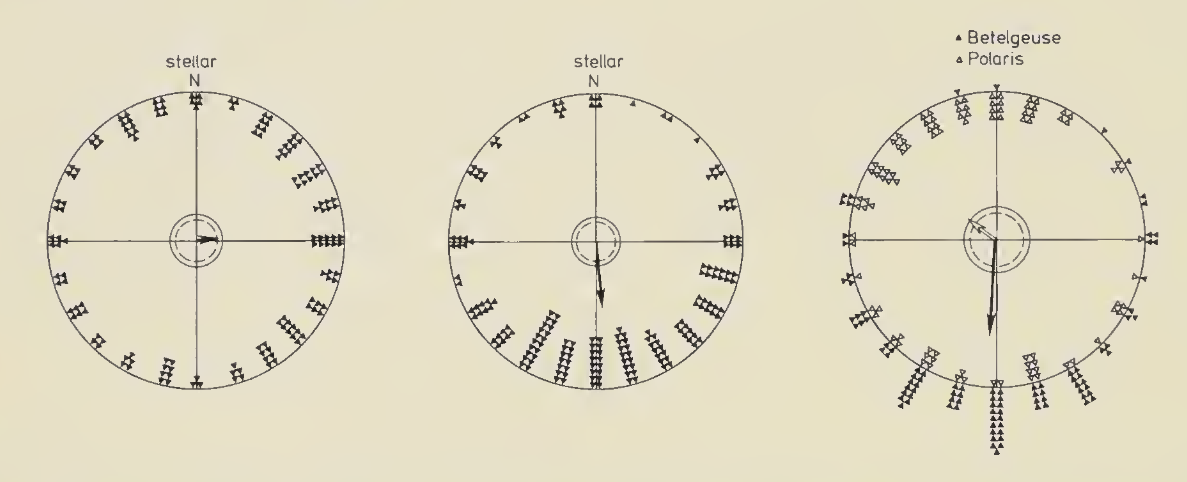


FIGURE 1. Pooled nightly headings of handraised Indigo Buntings tested during their first autumn migratory season under a stationary planetarium sky. Expected migratory direction: South. (a) Birds that had never seen any stars prior to the tests. (b) Birds that had seen a normal planetarium sky rotating around the north star Polaris. (c) Birds that had seen a planetarium sky rotating around Betelgeuse in Orion. Open symbols: data plotted taking Polaris as "North"; solid symbols: same data, replotted taking Betelgeuse as "North". (Redrawn from EMLEN 1972).
In this and the following figures, the arrows indicate the mean vector, their lengths being drawn relative to the radius of the circle = 1. The inner circles represent the 5% (dotted) and the 1% significance border of the Rayleigh Test.

WILTSCHKO & GWINNER (1974 and in prep.) performed similar tests with two groups of handraised Garden Warblers, *Sylvia borin.* One group never saw any celestial cues during their life, the second group had clear view to the natural sky until the beginning of the migratory season. In orientation tests in the natural local geomagnetic field, but without celestial cues, the birds of the first group showed a significant preference of their expected migratory direction (Fig. 2a), whereas in the birds that had seen the sun and the stars, no directional preference was found (Fig. 2b). This leads to the conclusion that in Garden Warblers the migratory direction is genetically encoded relative to a non-visual orientation system, and that the orientation in the absence of visual cues is not improved by celestial information.

Parallel experiments with the same species and with European Robins, *Erithacus rubecula,* both trapped during migration, suggest the magnetic field as the non-visual reference system for the migratory direction: disorientation was observed in a reduced magnetic field (WILTSCHKO 1974), and in outdoor experiments, we appeared to be able to

change the directional significance of the natural stars by exposing the birds to an altered magnetic field (WILTSCHKO & WILTSCHKO 1975 a,b). This led to the hypothesis that the magnetic field is used to calibrate the star patterns during migration. Since the directional significance of the stars could be altered even in adult birds, our results suggest that it is permanently controlled by the magnetic field, thus indicating a type of learning different from the imprinting-like process EMLEN (1972) described.

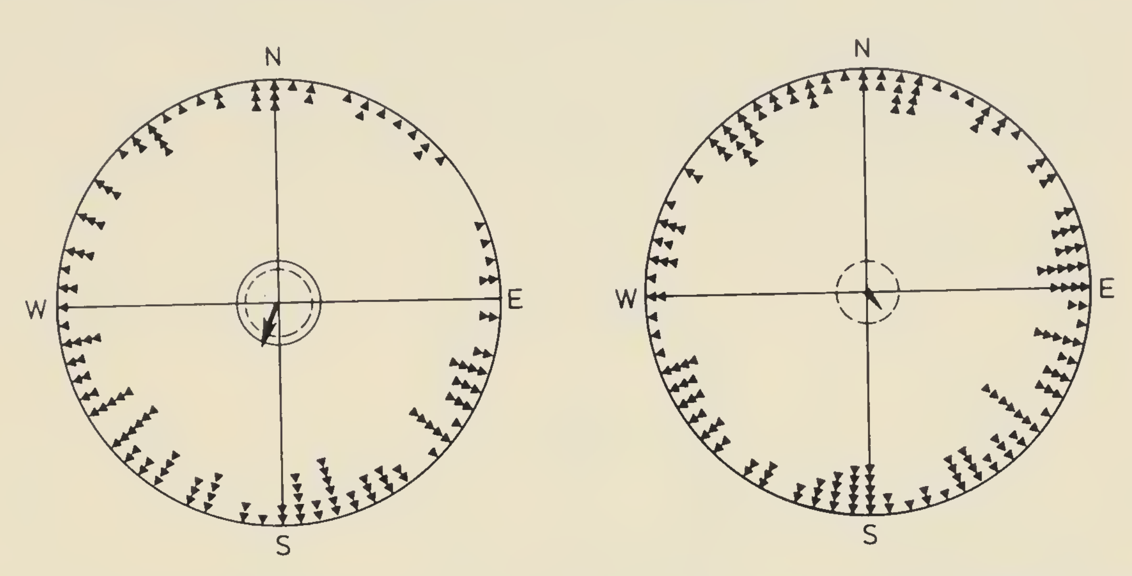


FIGURE 2. Pooled nightly headings of handraised Garden Warblers tested during their first autumn migratory season in the local geomagnetic field without visual cues. Expected direction: S to SSW. (a) Birds that had never seen any celestial cues. (b) Birds that had had view to the sun and stars until the beginning of the migratory season.

At the present state of knowledge, it is possible to explain the differences between EMLEN's (1972) and our findings satisfactorily in terms of species-specific differences. It may be pointed out, however, that in our experiments with handraised Garden Warblers, it is not excluded that these birds have any innate celestial orientation. The birds handraised with view to the stars oriented very poorly when these cues were no longer available (Fig. 2 b) – this phenomenon, which is not found in birds captured during migration, is still completely unexplained and might indicate that stars are somehow involved in the normal process of establishing the migratory direction. Similarly, the role of the magnetic field in the orientation of the Indigo Bunting is not yet completely understood. Recent findings that this species, too, is able to determine the migratory direction using magnetic information (EMLEN et al. 1976) make it desirable to study whether the magnetic field does function as a reference system for the innate migratory direction in the Indigo Bunting.

Day-migrating birds

Very little is known about the orientation mechanisms of day migrants. The sun compass is generally accepted as their principle orientation system (KRAMER 1950, EMLEN 1975), but experimental evidence that the sun compass is actually used to orient their activity during migration is almost entirely lacking. Here I will report some preliminary results of a study with handraised Finnish Starlings, *Sturnus vulgaris*, that from their fledging age on had been housed in an outside aviary so that they had view to the sky. We examined whether they utilized the sun for direction finding by shifting their internal

clocks 6 hours, a procedure which demonstrates the use of the sun compass by resulting in a 90° deflection of orientation (Hoffmann 1954, Schmidt-Koenig 1961).

The pooled results are presented in Fig. 3. In their first autumn migratory season, the Starlings showed a significant directional preference (Fig. 3 a,b), which did not correspond to their expected migratory direction WSW, although they had grown up and were living in more or less natural conditions seeing the sun. In the following spring, however, their directional tendencies (Fig. 3 d,e) agree well with the spring migratory direction of the Finnish population. In both seasons, the orientation behavior was not at all affected by cloud cover: it was just as good under overcast (Fig. 3 a,d) as under sun (Fig. 3 b,e). Thus Starlings do not seem to need the sun to show consistent directional selections.

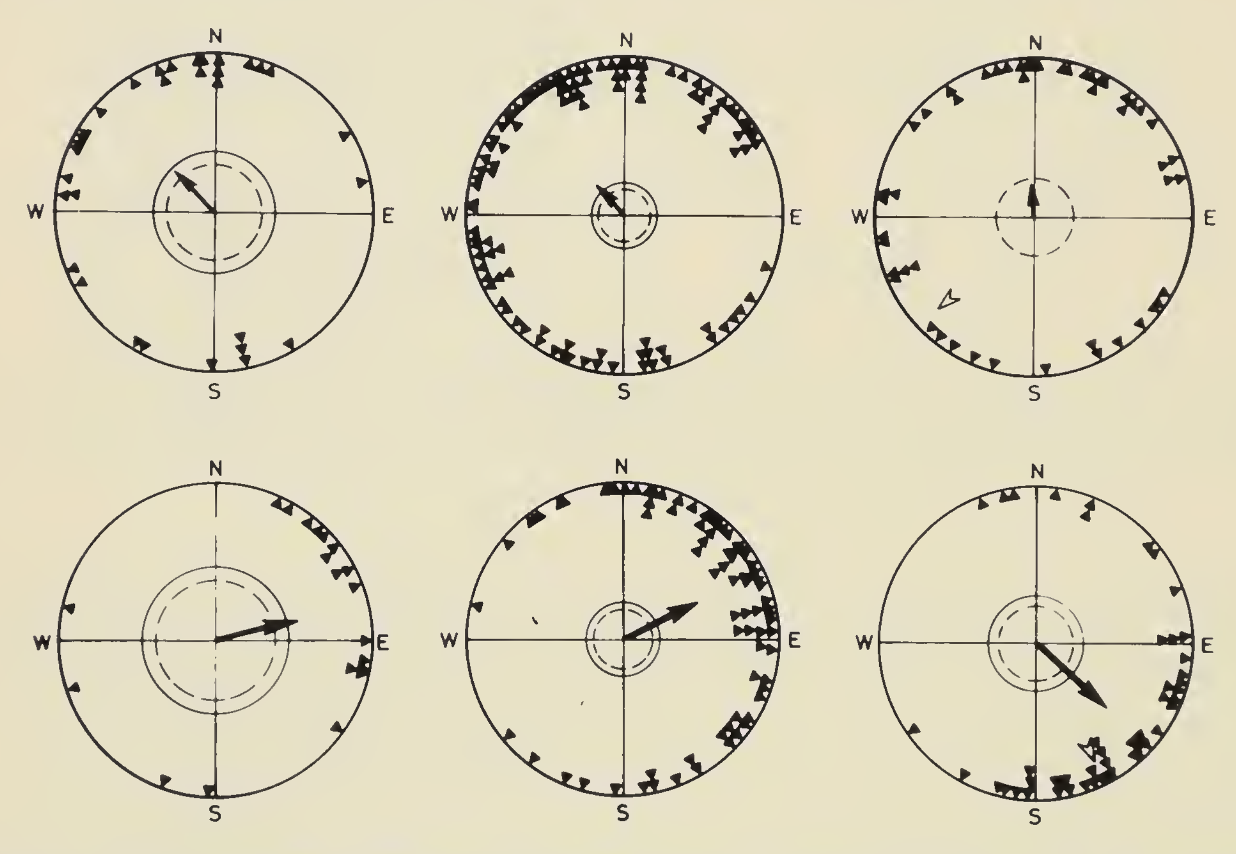


Figure 3. Pooled headings of handraised Starlings tested in outdoor experiments. Upper diagrams (a – c): tests during their first autumn migratory season, expected direction: WSW; lower diagrams (d –f): tests during the following spring, expected direction: ENE. (a) and (d): under complete overcast; (b) and (e): when the sun was visible; (c): under sunny conditions, the birds' internal clocks being shifted 6 h fast; (f): under sunny conditions, the birds' internal clocks being shifted 6 h slow. The open arrow heads inside the circle in Fig. 3 c and f mark the expected direction if the birds use a sun compass.

In autumn, a 6 h fast clock shift did not cause any deflection in the Starlings' directional tendencies, but only a small increase in scatter (Fig. 3c). In spring, however, a 6 h slow clock shift resulted in a significant ($p < 0.001$, Watson Williams Test) shift in the expected direction (Fig. 3f). With 76°, the amount of shift was slightly smaller than expected. Unfortunately, we had only 6 birds for our spring experiments, but an analysis of their individual behavior revealed considerable differences, their amount of shift varying between 30° and 97°. Each bird was subjected to the clock shift procedure three times, with intervals of ca. two weeks during which it lived in the natural photoperiod and was tested in control tests. A temporal analysis of our data seems to indicate that the deflection caused

by shifting the internal clocks was much more pronounced at the end of the season, the mean of the first, second and third shift deviating by + 43°, + 57° and + 86°, respectively, from the mean of the control recordings.

Thus we found no indications that in their first autumn migratory season, the Starlings utilized the sun for dirction finding. Our data indicate that they began to use it in the course of the spring migratory season. This seems to suggest that the sun compass requires some maturing or learning process. Since the sun compass of pigeons was found to be established by experience (WILTSCHKO et al. 1976) the orientation of our young Starlings appears to represent a parallel to the development of the sun compass in young homing pigeons (WILTSCHKO 1979). This leaves open the question of the reference system underlying this learning process. The non–visual orientation system used under overcast appears to be the most likely candidate, but an experimental analysis is still completely lacking.

Conclusion

The series of experiments discussed above indicate that such complex cue systems star patterns do not possess an innate significance, but that they acquire their directional meaning by some learning process. The same is possibly true for the complex, variable relationship between time, sun azimuth and direction in the sun compass. The two systems in consideration as underlying the calibration process – celestial rotation and the magnetic field – are of a simpler nature and thus theoretically better suited to serve as a reference system for the genetically encoded migratory direction. The experimental data so far do not allow any definite statement on which system plays the role of this basic reference system and whether it is the same in all species.

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SYMPOSIUM ON MECHANISMS OF GOAL ORIENTATION

9. VI. 1978

CONVENERS: K. SCHMIDT-KOENIG AND CH. WALCOTT

Olfactory and Magnetic Cues in Pigeon Navigation

F. Papi, P. Ioale', V. Fiaschi, S. Benvenuti and N. E. Baldaccini

Besides two mechanisms of compass orientation, namely the sun compass and the magnetic compass, homing pigeons possess a mechanism, the so-called "map component", which allows them to navigate, i.e. to detect the direction of their goal when released from unfamiliar sites. It is often claimed that this navigational system is redundant and flexible, and that it relies on a large variety of cues. This opinion, however, appears to overlook the principle of Ockham's razor, because, as regards cues involved in the "map component", the only evidence is that in favour of olfactory ones, with some indications in favour of magnetic ones.

The use of olfactory cues for navigational purposes in pigeons was first suspected seven years ago, when we found that birds which had had their olfactory nerves cut were greatly impaired in homing (Papi et al., 1971). Later, several experiments were performed on the effects of olfactory deprivation. The most frequently used methods for making the birds anosmatic were: a) bilateral sectioning of their olfactory nerves; b) sectioning of one nerve and occlusion of the contralateral nostril – a technique which allows comparison between experimental birds and control birds which have also undergone unilateral nerve section and occlusion of one nostril, in their case the ipsilateral – and c) insertion of thin plastic tubes into the birds' nostrils up to the choanae, so that inhaled air bypassed the olfactory chamber.

By all these methods we were able to confirm the earlier finding that anosmatic pigeons have great difficulty in homing when they are released from unfamiliar sites. From familiar ones, however, experimental birds performed only a little worse than control birds (Fig. 1). In our opinion, this shows that olfaction plays an important and specific role in pigeon navigation, because, if olfactory deprivation had produced only a non-specific disturbance in general behaviour, there should have been no differences in homing success from familiar and unfamiliar sites (for a review, see Papi, 1976, and the subsequent paper of Hartwick et al., 1977).

Olfactory deprivation also influences the initial orientation of the birds, which often fly off in a wrong or random direction. This effect, however, was less consistent in some experimental series (see, in this volume, Benvenuti et al., who survey the apparant differences in behaviour of pigeons tested in different countries), Schmidt-Koenig & Phillips (1978, in press) used a local anaesthetic, xylocain, to eliminate olfaction transitorily. They claim that in homing experiments "only slight and inconsistent effects" were found. In our opinion, however, no definitive conclusions are possible. In fact, in their first experimental series, treatment with xylocain was found to have a significant effect in three out of the four experiments performed on new-to-site birds. In the second series, the control bird bearings were mostly random, and, as the authors admit, were "a poor basis on which to find an experimental effect".

The results obtained with anosmatic birds provide some of the main evidence in favour of the olfactory hypothesis of pigeon navigation (Papi et al., 1972). According to this

Istituto di Biologia Generale dell' Università di Pisa, Pisa, Italy

hypothesis, pigeons learn to recognize the prevalent odour of their loft area and also to associate foreign odours carried by winds with the direction from which they come. In this way the birds are thought to build up an olfactory map of the region surrounding the loft. When displaced to an unfamiliar site the birds could then determine the home direction by means of the odours perceived in the release area and during the outward journey (for a full explanation of this hypothesis, see PAPI, 1976).



FIGURE 1. Homing performances of anosmatic birds released from unfamiliar and from familiar sites. Each symbol represents one pigeon; empty symbols for controls, filled symbols for experimentals. The data concern experiments performed in Italy (PAPI et al., 1971, 1972; BENVENUTI et al., 1973, except the inexperienced birds; BALDACCINI et al., 1975; HARTWICK et al., 1977), in Switzerland (FIASCHI & WAGNER, 1976), in USA (PAPI et al., in prep.), and in Germany (BENVENUTI, unpublished results of research still in progress).

The olfactory hypothesis is consistent with the results obtained by WALLRAFF (1966, 1970), which showed that homing capacity is very poor in pigeons kept in aviaries fenced against wind, as well as with the results of a variety of experiments we performed specifically to test predictions derived from the hypothesis (reviewed in PAPI, 1976). In some of these experiments, we deceived the birds about the direction from which the wind-carried odours arrived at the loft by rearing them in large outdoor cages supplied with deflector shields. Depending on their arrangement, they systematically deflected the wind before it reached the cages, clockwise or counter-clockwise. The pigeons kept in these cages showed a corresponding deflection in their initial orientation (BALDACCINI et al., 1975b, 1978).

The results of the deflector cage experiments are in agreement with the olfactory hypothesis, but do not prove unambiguously that the stimuli deflected by the shields and involved in the deflector cage effect are really the odours carried by winds, because also other stimuli – sounds, for example – are deflected by the shields. We have therefore performed new experiments in which pigeons were no longer exposed to natural winds, but were exposed to artificial air currents produced by fans. The birds were kept in glass corridors, which had large fans at both ends. The main axis of the corridors was oriented

East-West. Whenever a wind was blowing from the East or the West quadrant, the birds of one corridors (the controls) were exposed to fan-produced wind blowing from the median bearing of the same quadrant, whereas the birds in the other corridor (the experimentals) had a wind blowing towards them from the opposite direction. In the two series of these experiments performed by us, an additional group of birds kept in a third corridor without fans were also tested. In one series these birds were exposed to the natural winds from both the East and West quadrants (control-controls), whereas in the other series they were never exposed to either natural or artificial winds ("screened" birds).

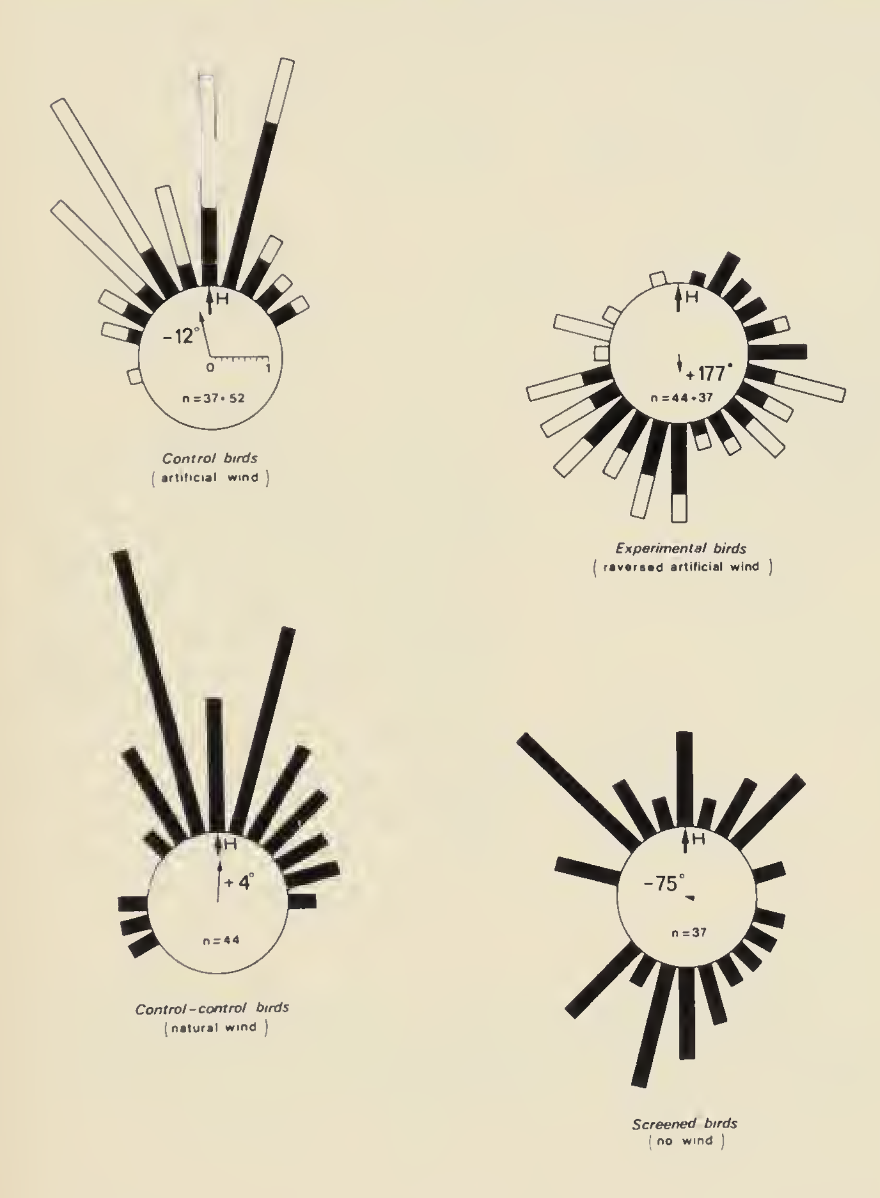


Figure 2. Initial orientation of the birds kept in glass corridors in releases from East and West. For each treatment the data were pooled, setting the home direction (H) to zero. The length of the bars in proportional to the percentage of bearings occurring in each 15° sector. For the birds of the fan corridors (top), the data comprise two series of experiments; in each bar the empty portion refers to one series, and the dotted portion to another. The inner arrow represents the mean vector, whose length can be read with the scale in the first diagram. The number of bearings (n) is given. (According to data from Ioale' et al., in prep.).

The initial orientation of the birds in the releases from East and West is shown in Fig. 2. The control birds and the control-controls were homeward oriented, whereas the experimentals, which were rather more scattered, departed in the opposite direction from the homing one. Finally, the "screened" birds were randomly oriented. These results greatly reduce the number of stimuli which may be thought to be involved in the deflector cage and support the view that the information that pigeons acquire at the loft and then use for navigational purposes is wind-borne and involves the sense of smell.

Despite the large quantity of evidence in favour of olfactory navigation, some reasons for believing that magnetic stimuli also influence pigeon navigation may be put foreward. Cornell investigators reported that there is a correlation between normal fluctuations in the earth's magnetic field and day-to-day variations in the pigeons' initial orientation, and that

this correlation reflects a cause-and-effect relationship (KEETON et al., 1974; LARKIN & KEETON, 1976). Still more impressive is the fact that at the recent Conference on Animal Migration, Navigation and Homing (Tübingen, 1977), investigators from three different laboratories reported some evidence that magnetic stimuli perceived during the outward journey influence pigeons' initial bearings (KIEPENHEUER, 1978a, WILTSCHKO et al., 1978; PAPI et al., 1978; see also KIEPENHEUER, 1978b, and in this volume). The method used by our team consisted in transporting two groups of pigeons to the same release site – a group of controls inside an aluminum container and a group of experimentals in an iron container. Forced ventilation was provided for both containers, but the strength of the earth's magnetic fields was reduced to 1/200 of its natural value inside the iron one.

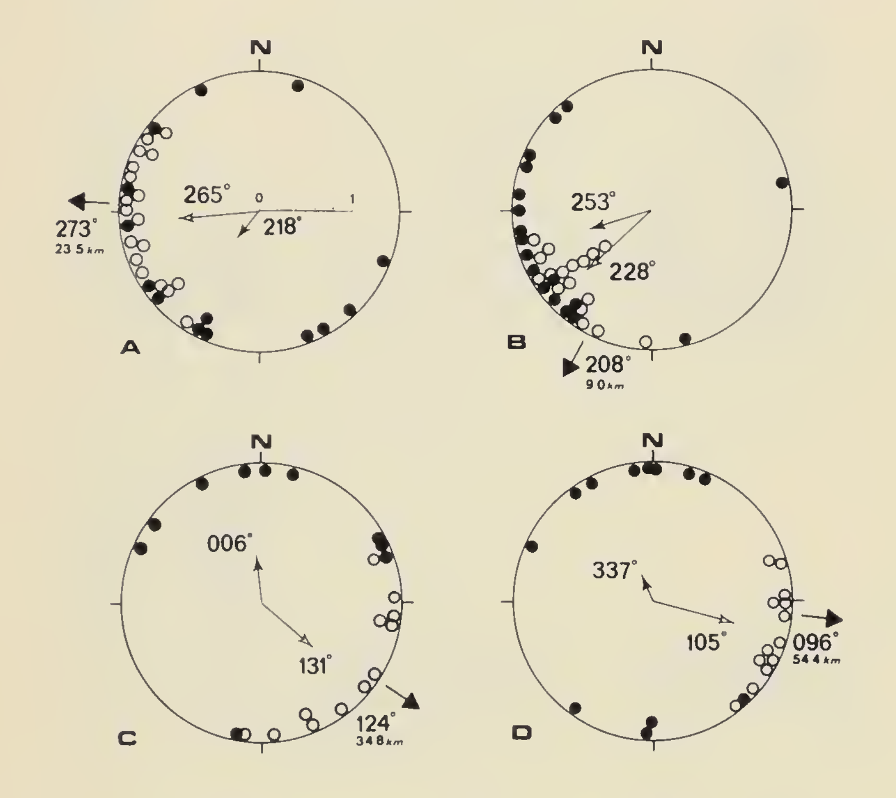


FIGURE 3. Effect of the iron container on initial orientation. A and B, veteran birds released from short distances; C and D, young birds. Each symbol on the periphery of the circles indicates the vanishing bearing of one bird, the inner arrows represent the mean vectors. Empty symbols for controls, filled symbols for experimentals. The outer arrow indicates home, whose direction and distance are given.

In the first series of experiments, we trained the birds to home in one direction and then performed the experiments in the opposite one, from distant sites beyond the Appenines. In this case there was a dramatic difference in initial orientation between controls and experimentals (see PAPI et al., 1978). In the second series of similar experiments, veteran birds which had not been so trained were released from short distances; the iron container was again found to have an effect. The difference in initial orientation, however, was smaller and more variable than in the first series (see for example Fig. 3 A, B). Lastly, we performed a series of tests with young birds which had been previously trained to home in all directions from distances up to 30 km. When released from unfamiliar sites, a clear-cut difference in orientation between control and experimental birds was found even at short or moderate distances (examples are given in Fig. 3 C, D).

It is very surprising that in all our experiments with aluminum and iron containers, we never found a significant difference in homing performance between control and experimental birds. We must therefore conclude that the experimentals were able to correct their wrong starting direction quickly. This makes the interpretation of the "iron container effect" even more difficult.

Our still inadequate understanding of the role magnetic cues play in pigeon navigation makes any discussion about the possible interaction between olfactory und magnetic cues a difficult matter. We know that pigeons are incapable of homing from unfamiliar sites when they are prevented from smelling; unfortunately we have not yet been able to devise a method for isolating birds from the earth's magnetic field when they are in flight, which is a necessary precondition for weighing one cue against the other.

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Pigeon Homing: A Comparison Between Recent Results Obtained in Different Countries

S. Benvenuti, N. E. Baldaccini, V. Fiaschi, P. Ioale' and F. Papi

The much debated question whether there are important differences between the physical substrate patterns which provide navigational cues in various regions has become more pressing now that it has been shown that alfactory cues are necessary for correct orientation and successful homing in pigeons (for a review, see Papi, 1976). In fact, some of the first attempts made abroad to repeat the experiments of the Italian investigators, which supported the hypothesis of pigeons navigation by olfactory cues, produced negative or inconclusive results, and suggested that olfactory information might only be useful to pigeons which live, like Italian ones, in areas particularly rich in aromatic vegetation (Keeton, 1974; Krebs, 1975; Keeton & Brown, 1976). In this view, pigeons of different regions rely for their navigation on cues of different nature. This hypothesis, however, seems improbable to us after considering the results of experiments recently performed or in progress in Germany, Switzerland and in the United States. It is aim of the present paper to survey these results and compare them with those obtained in analogous experiments carried out in Italy.

The experiments which are auitable for comparison may be divided into four groups: a) those in which olfactory perception is disturbed at the release site, b) those on anosmatic birds, c) those involving detours, and d) those using deflector cages.

Experiments based on disturbance of olfactory perception at the release site.

The olfactory hypothesis implies that olfactory stimuli experimentally added to the natural ones should disturb the perception of the olfactory cues used by pigeons for navigational purposes. The first experiments performed in Italy by applying strong odorants (α-pinene and other substances) on or near the birds' nostrils gave positive results. The treatment, however, disturbed the birds' behaviour in a variable and unpredictable way (Benvenuti et al., 1973). Later experiments, in which the birds were also prevented from perceiving olfactory cues in the regions crossed during the outward journey, gave clearer results. In fact, their initial orientation was consistently disturbed. In both series, homing performance was, as a rule, impaired too (Benvenuti et al., 1977). In Switzerland Fiaschi & Wagner (1976) obtained positive results by using α-pinene and by transporting pigeons with their nostrils free. In New York state, on the other hand, Cornell pigeons' initial orientation was not influenced by application of α-pinene, either in a first experimental series (performed by transporting the birds to the release site with their nostrils free, Keeton & Brown, 1976), or in a second series (birds transported with nasal plugs, Papi et al., in prep.). In the second series, however, the experimental birds had rather longer homing times than control birds.

In Germany, application of odorants (α-pinene and menthol) near to the birds' nostrils gave negative results (Hartwick et al., 1978 in press).

Istituto di Biologia Generale dell' Università di Pisa, Pisa, Italy

Olfactory deprivation experiments.

Several techniques have been used in order to prevent homing pigeons from smelling: a) bilateral severance of olfactory nerves, b) severance of one olfactory nerve and plugging of the contralateral nostril, c) insertion through the choanal opening of plastic tubings, which were sealed in the nostril so that air could only get in through the tubes, bypassing the olfactory chamber, and d) plugging of both nostrils. With all these techniques, the elimination of olfactory ability has always greatly impaired pigeon homing from unfamiliar localities in all the countries where experiments have been performed (Italy: PAPI et al., 1971, 1972; BENVENUTI et al., 1973; BALDACCINI et al., 1975a; HARTWICK et al., 1977; Switzerland: FIASCHI & WAGNER, 1976; Germany: unpublished results of one of ours (S.B.); New York state: KEETON & HERMAYER, personal communication, KEETON et al., 1977; PAPI et al., in prep.; Utah: SNYDER & CHENEY, 1975). Olfactory deprivation also disturbed initial orientation, so that the birds departed in a wrong or random direction. In New York state and Germany, however, this second effect was sometimes not very clear, or was masked by the random orientation of the control birds, or was absent. For this reasson we use ± to indicate the effect of olfactory deprivation on German and Cornell pigeons in Table 1.

TABLE 1: Results of the experiments in different countries.

	I	CH	D	N.Y.	Utah
Disturbance of olfactory perception	+	+	–	–	
Olfactory deprivation	+	+	±	±	+
Detour experiments	+	+	+	+	
Deflector cage experiments	+		+	+	

Detour experiments.

If two groups of pigeons are transported simultaneously to the same release site by different routes, with the first segments of the two routes diverging strongly, the birds are often differently oriented (Fig. 1). In fact, they show the tendency to depart in a direction opposite to that of the first leg of their outward journey (PAPI et al., 1973, 1978; PAPI, 1976). Therefore, one group deflects clockwise and the other counterclockwise. The detour effect may be attributed to the odours perceived during the initial part of the outward journey which are more familiar. This agrees with the fact that the detour effect is absent in birds prevented from smelling during the outward journey.

For unknown reasons, the detour effect is variable, and only some kinds of detour produced a significant difference in the initial orientation of the two bird groups. In Italy, 27 detour experiments on new-to-site birds were performed using 12 kinds of detour. In 17 cases a significant difference in the orientation between the two groups was found. In Switzerland, one detour experiment performed by FIASCHI & WAGNER (1976) produced the predicted effect, while in Germany, HARTWICK et al. (1978, in press) were able to find only one site, out of 12 experimented, in which Frankfurt birds consistently revealed a significant deviation from the predicted directions. However, pooling the data of all their

experiments, two bearing distributions were found, the mean vectors of which were significantly different.

In New York state some detour experiments were first performed by KEETON (1974) with negative results. However, in a second series of experiments, performed by KEETON & BROWN together with two of us (S.B. and F.P.) the effect of three new kinds of detours was tested, and it was found that one of them produced the expected deflection, in the first experiment and in its repetition (PAPI et al., in prep.).

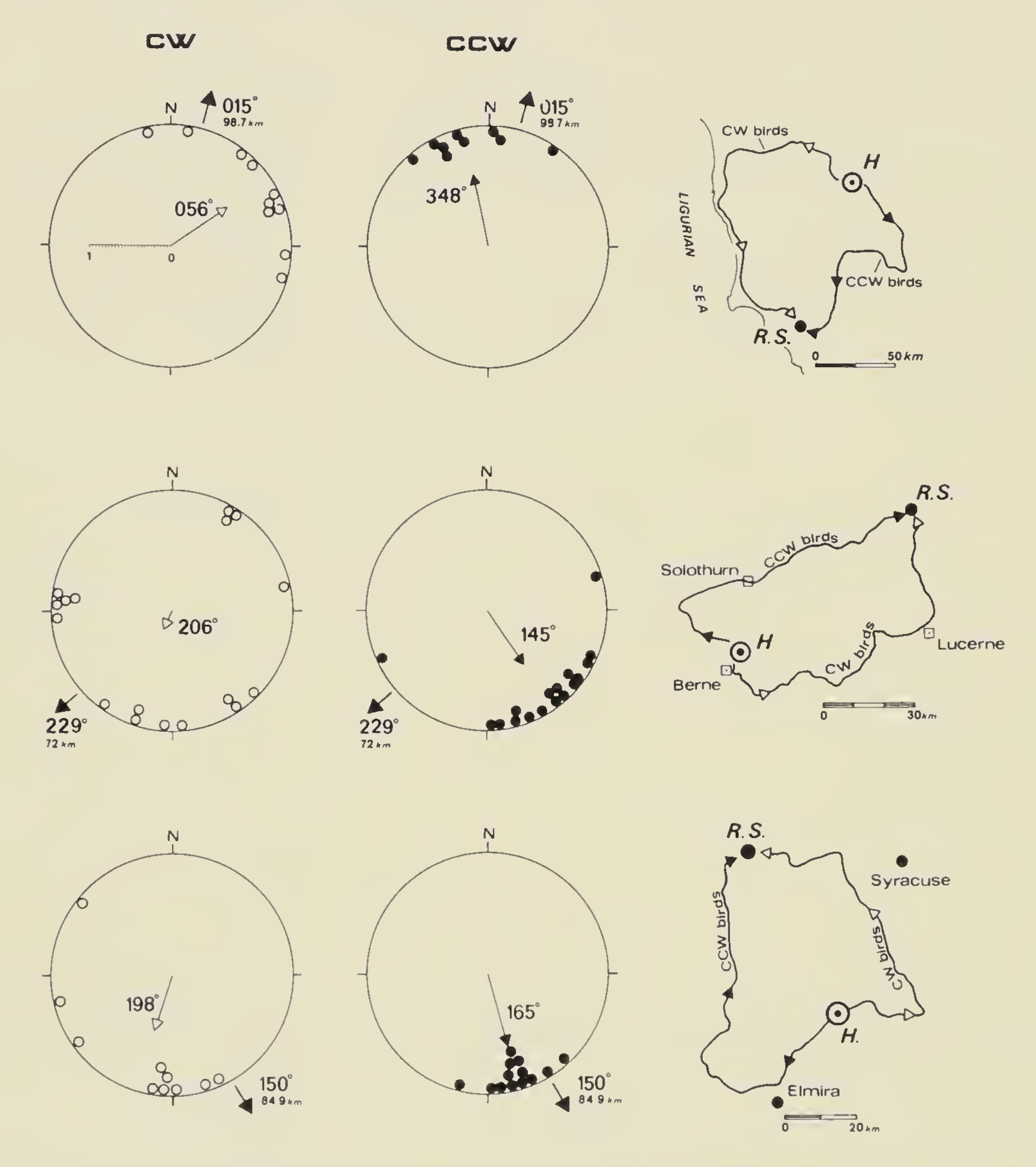


FIGURE 1. Three detour experiments, performed in Italy (top), in Switzerland (center), and in New York state (bottom). In each experiment two groups of birds were transported from home to the release site following the two routes indicated in the map. Each pair of circular diagrams shows the initial orientation of the group expected to deflect clockwise (CW, on the left) and of the group expected to deflect counter-clockwise (CCW, on the right). Each symbol on the periphery of the circles indicates the vanishing bearing of one bird. The inner arrow gives the mean vector, whose length can be read with the scale in the first diagram; the outer arrow indicates home, whose direction and distance are given (from PAPI, 1976; FIASCHI & WAGNER, 1976; and from PAPI et al., in prep.).

Deflector cage experiments.

In agreement with the olfactory hypothesis, pigeons reared in large outdoor cages, fitted with wind deflectors producing a clockwise or counter clockwise deflection of the wind

before it reaches the cage, are expected to show a corresponding deflection in their mean bearing at the release site. The positive results obtained in Italy are reported in the papers of BALDACCINI et al. (1975b, 1978), and PAPI (1976). Recently, deflector cages identical to those used by the Italian investigators have also been employed in Germany and in the United States. Reports of these results, agreeing with those obtained in Italy, will soon be published (KIEPENHEUER, personal communication, WALDVOGEL et al., in prep.). Fig. 2 shows some of the results obtained in these three countries.

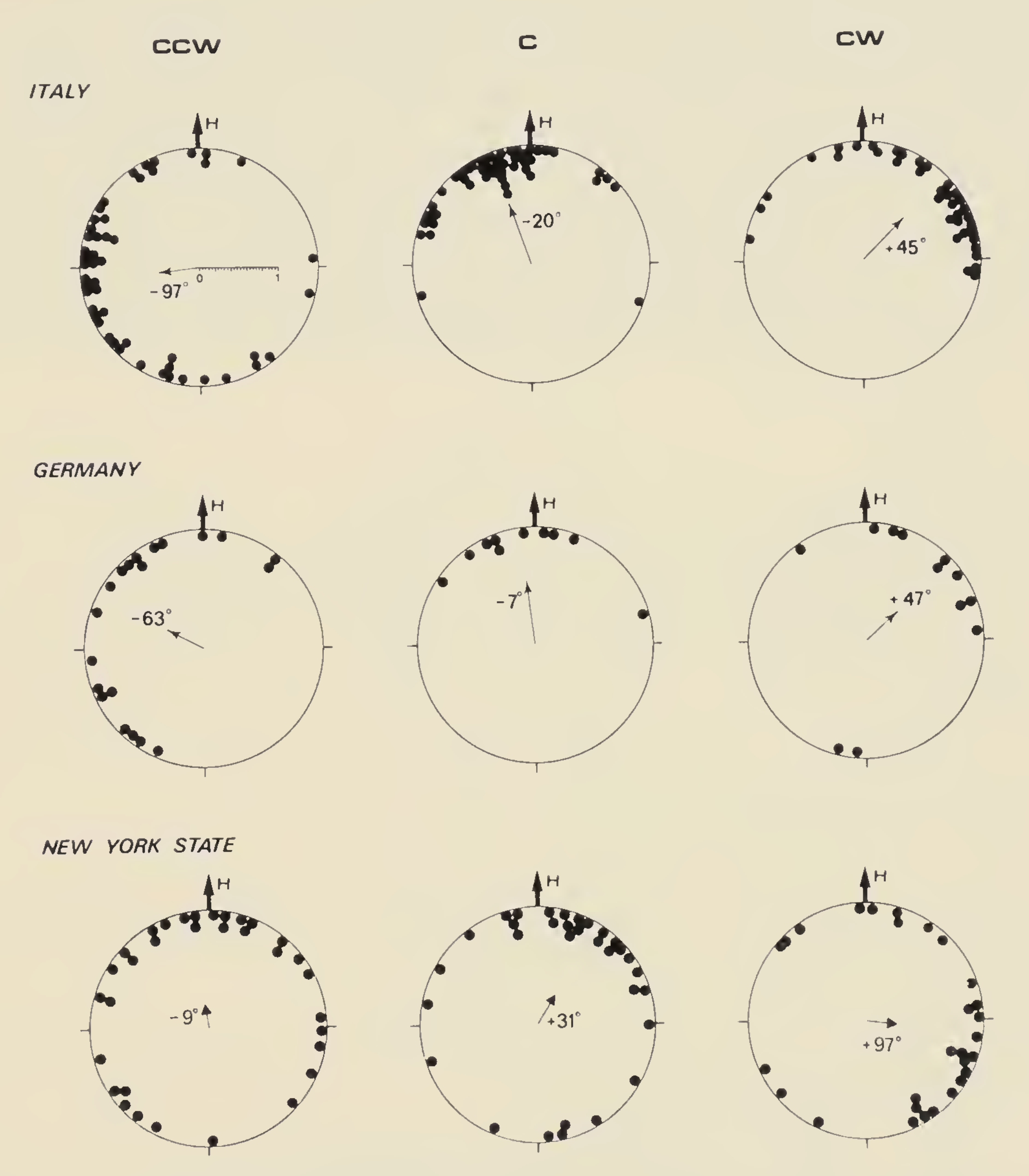


FIGURE 2. Initial orientation of the birds from deflector cages. Results obtained in Italy (BALDACCINI et al., 1975b), in Germany (J. KIEPENHEUER, personal communication) and in New York state (PAPI et al., in prep.; the data refer to the birds at their first flight). In each horizontal row, the bearings of the experimentals expected to deflect counterclockwise (CCW) and clockwise (CW), as well as those of the controls (C) are shown. Home direction (H) has been set to zero. Other explanations as in Fig. 1.

Conclusions.

From the facts reported above, it appears that pigeons' dependence on olfactory cues for navigation is a general phenomenon and that is not restricted to some areas. This conclusion is mainly supported by the fact that anosmatic pigeons are always greatly

impaired in homing from unfamiliar sites. The similarity in the results obtained in different countries with the detour and deflector cage experiments stands as further evidence that the same homing mechanisms are operative in pigeons of different areas.

The initial orientation of pigeons in Germany and New York state, however, appears to be only slightly affected by treatment with odorants and by olfactory deprivation. In our opinion, this may be related to the fact that in these areas even normal (i. e. unmanipulated) pigeons are often randomly oriented or have a strong orientational bias. Because recent experiments performed by exchanging young German and Italian pigeons failed to show genetic differences in the homing behaviour (unpublished data), we suggest that the differences observed are due to regional differences in concentration of natural odours and/or to different techniques of rearing and training, especially if these involve differences in degree of exposure to winds. On the other hand, as recently emphasized by WALLRAFF (1978, in press), the direction chosen by displaced pigeons at departure may depend upon several circumstances. Recent findings also indicate the possible influence of magnetic cues detected en route (see the papers of PAPI & KIEPENHEUER in this volume). So it may well be that the factors influencing the orientation of pigeons have a different relative importance in different areas.

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On the Role of Olfactory Cues in Pigeon Homing

K. Schmidt-Koenig

Introduction

In recent laboratory cardiac conditioning experiments (Schmidt-Koenig & Phillips, 1978) xylocain spray was shown to eliminate olfaction in pigeons for 60–90 min. This technique of local anesthesia has the advantage of being reversible, not interfering with breathing and being at best only mildly traumatic as compared to inserting nasal tubes or surgically dissecting the olfactory nerve (Papi et al., 1971; Benvenuti et al., 1973; Keeton et al., 1977; Hartwick et al., 1977; Hermayer & Keeton, ms. in prep.). While more laboratory experiments are in progress to test other, longer lasting local anesthetics, additional homing experiments were carried out in Sept. 1977 with xylocain spray to test the effect of eliminated olfaction at shorter releasing distances (25 km) than used previously (40 km and 70 km) and entirely untreated birds were used as "super-controls".

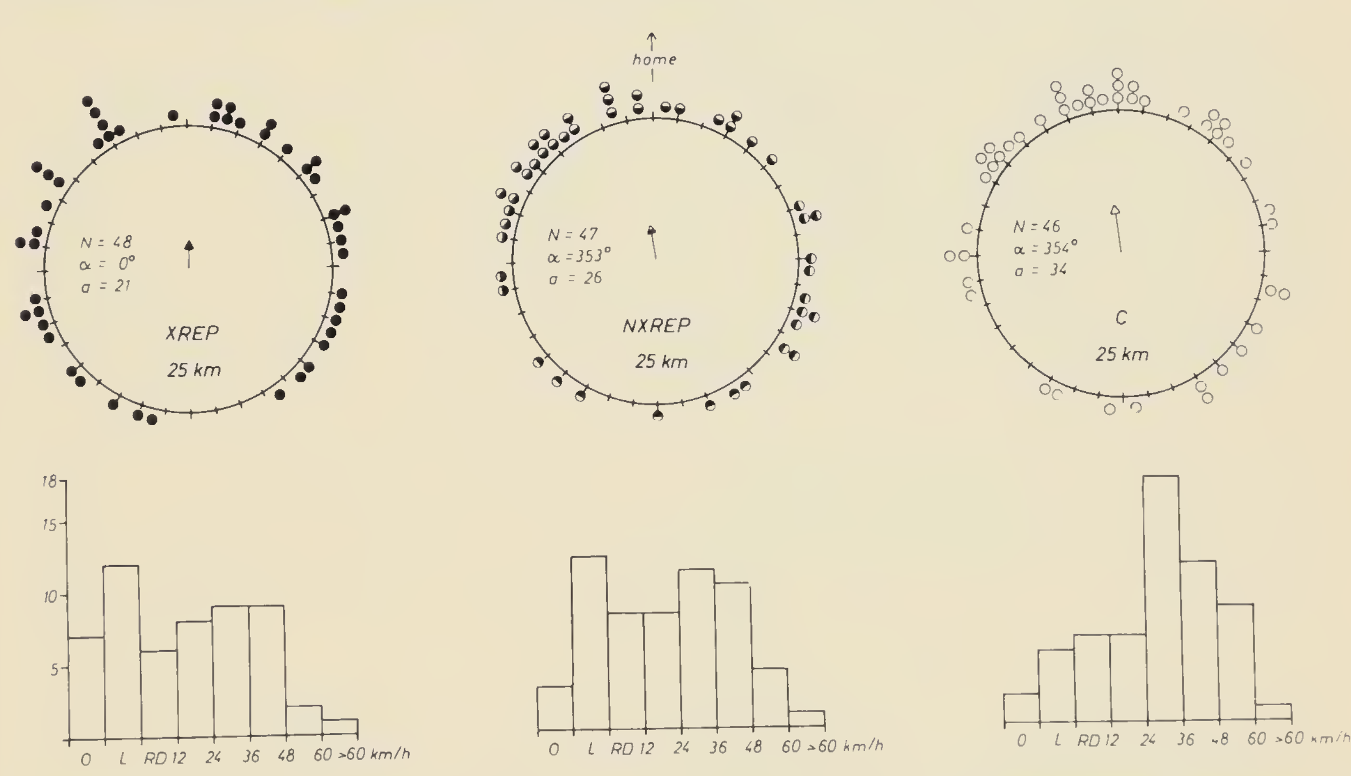


Figure 1. Summarized initial orientation (circular diagrams) and homing performance (histograms) of four releases from 25 km. XREP, xylocain repeatedly; NXREP no-xylocain repeatedly; C, untreated controls. Direction of the mean vector (α), its length (a) and sample size (N) are given in the circular diagrams. Homing performance has been summarized in eight classes of 12 km/h and below 12 km/h in class RD, homed on the day of release; L, homed after the day of release; O, never homed.

Methods and birds

Commercial xylocain spray was used. I am indebted to Astra Chemicals, Wedel, W-Germany for supplying no-xylocain spray identical to the commercial preparation lacking only the local anesthetic component. The spray, reduced from human oto-laryngeal dosage, was applied through the choanal opening.

Universität Tübingen, Abt. Verhaltensphysiologie 7400 Tübingen, Bundesrepublik Deutschland, and Dept. of Zoology, Duke University, Durham, N.C., USA.

One round of 4 releases was performed from 25 km distance in the cardinal compass directions with three groups of experienced birds. Experimental birds (XREP) were sprayed with xylocain before dixplacement and repeatedly every 75 min until the last bird was released. Likewise, control birds (NXREP) were treated repeatedly with no-xylocain spray. Super-control birds (C) remained entirely untreated. Treatment was rotated among the three groups. The birds were transported to the release site in crates in the open on a rack of a VW bus or inside a passenger car with windows rolled down. Initial orientation was recorded by field glass observation and precessed vectorially in the usual manner. Homing performance was timed and calculated in km/h (e.g. Schmidt-Koenig & Phillips, 1978).

Initial orientation was tested with the Rayleigh-test for randomness, the V-test for homeward directedness, the Watson U^2 test for inter-sample differences (e.g. Schmidt-Koenig, 1975, Appendix). Homing performance was tested with the Mann-Whitney U test (Siegel, 1956).

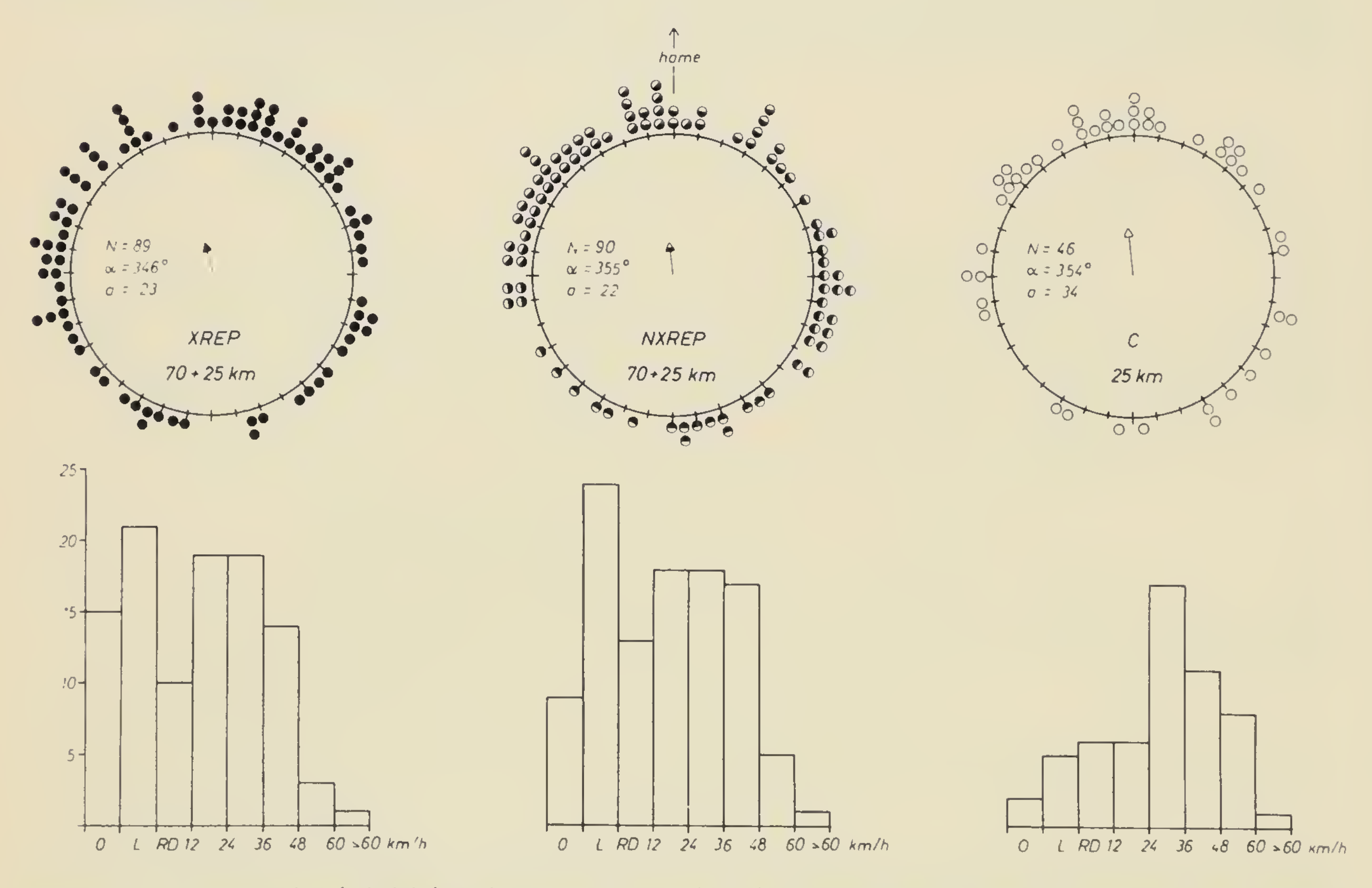


Figure 2. Summarized initial orientation (circular diagrams) and homing performance (histograms) of all 8 XREP and NXREP releases from 25 and 70 km and of the 4 releases of untreated controls from 25 km. Symbols as in Fig. 1.

Results

Initial orientation and homing performance are summarized in Fig. 1. In the 4 single releases initial orientation was never significantly different ($p>0.05$) among the groups; non-randomness and hemeward directedness of bearings were only exceptionally significant ($p\leq0.01$). In the summarized diagrams (Fig. 1) the XREP were nonrandom at $0.05>p>0.01$ and homeward-directed at $p>0.05$; the NXREP were nonrandom at $p<0.01$ and homeward directed at $p=0.05$; the controls were nonrandom and homeward directed at $p<0.01$. This apparent superiority of NXREP and of super-controls over XREPs was so

marginal that the Watson test does not detect any difference among the groups ($p>0.05$). There continues to be no difference ($p\gg0.05$) when the present data from 25 km are summarized with the previous data from 70 km (the 40 km do not qualify for summarizing because treatment was different). This summary is given in Fig. 2. In all three diagrams birds are homeward-directed ($\leqq0.01$) and at least marginally nonrandom ($0.05>p>0.01$ or better).

Homing performance of XREPs was inconsistent. It was very poor in one of the four 25 km releases ($p<0.01$ against the controls) and inferior to controls in another release with marginal significance ($p=0.03$) both producing a difference between XREP and controls in the summarized diagram (Fig. 1) at $p<0.01$. NXREP and XREP were not different ($p>0.05$).

Discussion and conclusion

Previous experiments (Schmidt-Koenig & Phillips, 1978) were designed to eliminate the perception of olfactory cues in experimental birds during the outward journey, according to Papi et al. (1972) that portion of the homing process during which pigeons identify local odors and the direction of displacement. The elimination of olfaction had only slight and inconsistent effects on initial orientation and homing performance. The homing experiments with repeated application of xylocain were designed to eliminate olfaction in the experimental birds during the outward journey, the waiting period at the release site and for as much of the homing flight as the remaining local anesthetic effect of xylocain would last. This treatment clearly did not have any negative effect on initial orientation. There was some effect on homing performance if treated birds and untreated controls are compared but this effect was not consistent. These results may be considered to be somewhat similar to those of Keeton et al. (1977) in experiments with birds with nasal tubes. The present results continue to support the view that olfactory information may be considered a factor of second order importance but it is not an essential element in pigeon homing. Birds without olfactory input like control birds have no difficulties selecting the home direction upon release homing.

Acknowledgment

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New Sensory Cues for Bird Navigation

Melvin L. Kreithen

Introduction

If you had King Solomon's ring, what questions would you ask?

By using very simple cardiac conditioning methods, it is possible to ask a bird questions about what it can sense. The bird answers these questions by increasing its heart rate whenever it detects a new stimulus. By asking questions in this way, I have been able to show that homing pigeons are sensitive to ultraviolet light, polarized light, atmospheric pressure changes, and infrasounds. These are only laboratory tests, but they have opened our minds to a wealth of new possibilities that were beyond our imagination just a few years ago. I would like to review these results and to point out areas for future research in the light of these new discoveries. I will be brief and therefore suggest that readers interested in further details use the included references.

Vision

It has always been assumed that ultraviolet (UV) light was only detectable by insects and that vertebrates are UV blind. Unless we use special instruments we cannot see the "invisible" UV patterns on flowers, on insects, and in the sky (Fig. 1). We have known that ants and bees can see patterns of polarized light and UV light in the sky and use it for their orientation (von Frisch, 1967). We have been led to believe that these cues are not used by any vertebrate animal.



Figure 1. Patterns of flowers and insects with visible and with UV light. Cameras fitted with quartz lenses, UV sensitive emulsions and filters can reveal patterns in UV light which are invisible to us.
Photos: T. Eisner, Cornell University.

Everything is now changed. A simple experiment in my laboratory showed that homing pigeons are remarkably sensitive to UV light. In another experiment a few years earlier, I showed that pigeons could detect polarized light as well. In many ways, the vision of birds

Section of Neurobiology and Behavior, Cornell University, Ithaca, New York, USA.

is more like insects than our own (KREITHEN & EISNER, 1978; KREITHEN & KEETON, 1973). Figure 2 shows the color responses of pigeons to both UV and "visible" light. There are two sensitive regions, one in the blue green (similar to our own vision) and one sensitive region in the UV at 350 nm. The 350 nm region is completely invisible to humans. I often look into the test chamber when the bird is responding to the UV light and I am frustrated when I can see nothing at all.

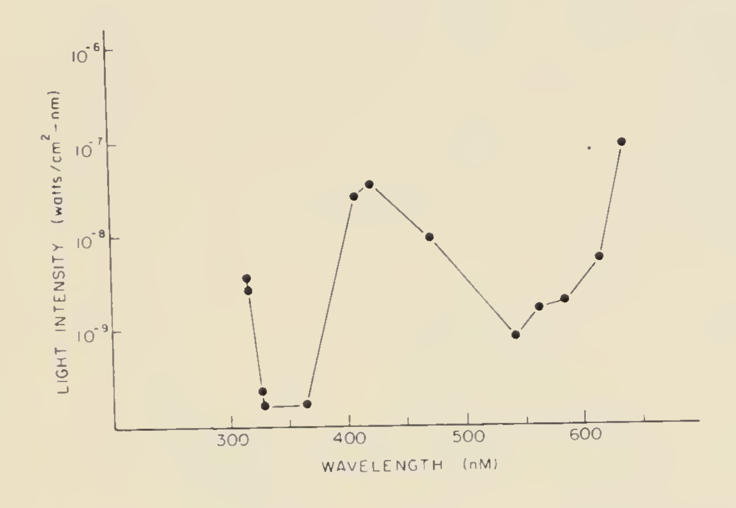


FIGURE 2. Spectral sensitivity of a pigeon to UV and visible light. Each dot is the threshold for light detection at each wavelength tested. Yellow pigments in the human lens prevent light of less than 400 mm from reaching our retinas. Birds, however, do not have these pigments and UV light can and does reach their retinas.

I have watched the birds perform another remarkable feat; they can see images using UV light alone. Three of my pigeons were tested, again with cardiac conditioning methods, with a simple visual task requiring visual acuity. The birds watched small targets (dark crosshairs on a light background) as indicated by a heart rate increase, when these targets moved across the screen. The crosshairs are less than 1 mm wide and are 50 cm from the bird's eye. This is sufficient acuity to resolve features on the antennae of butterflies.

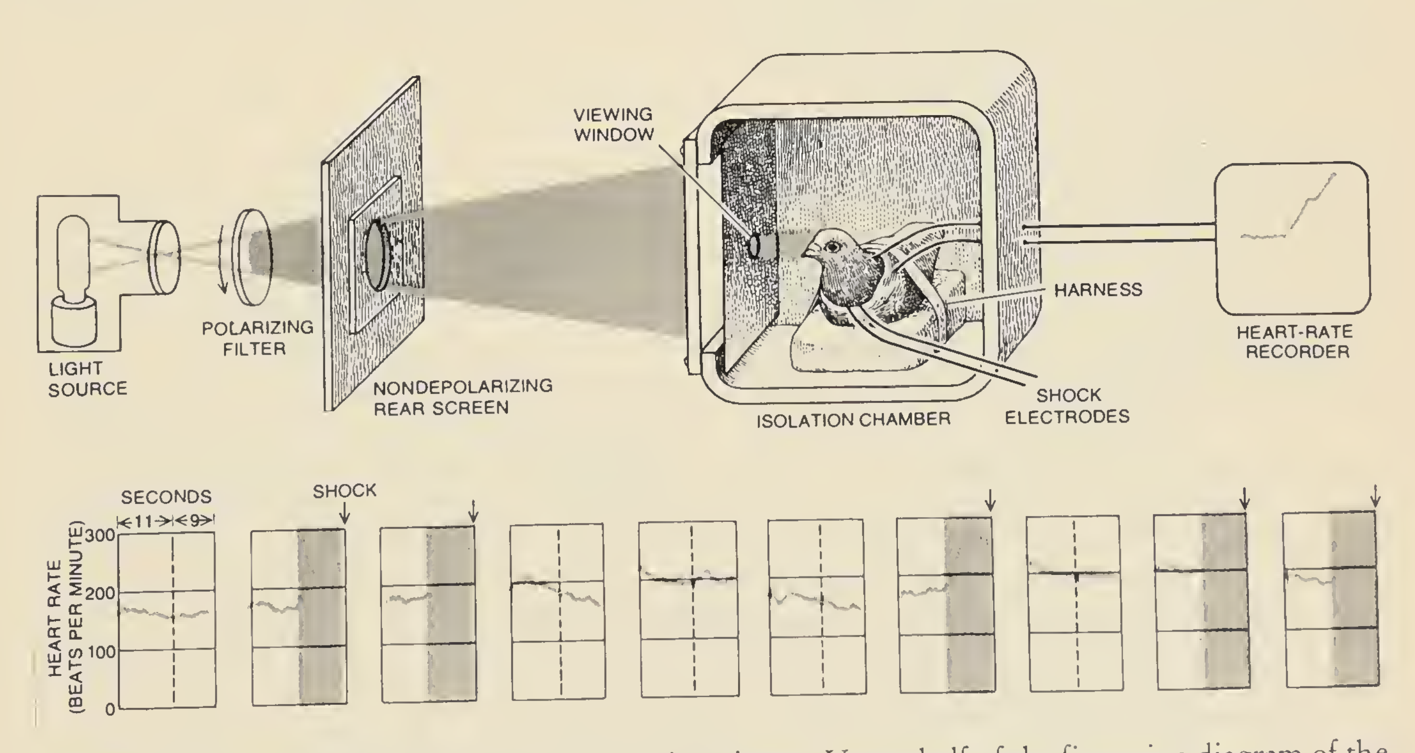


FIGURE 3. Polarized light detection by the homing pigeon. Upper half of the figure is a diagram of the testing apparatus. Lower half are 1) heart rate responses to test trials (shaded) – polarizing filter rotates followed by a mild shock; and 2) responses to control trials (unshaded) – no rotation and no shock. Only visible wavelengths were used as this was prior to the discovery of UV sensitivity. Copyright Scientific American, December, 1974. All rights reserved.

What is the meaning of these findings for the future of ornithological research? It is clear that birds can detect UV light and polarized light – even if we can't. What other birds besides pigeons have these senses? UV vision has only been tried with pigeons, crows, and hummingbirds (Kreithen & Eisner, 1978; Delius et al., 1978; Verheijen, pers. comm.; Huth & Burkhardt, 1972). Polarized light has only been tried with pigeons (Fig. 3) – what about all of the other birds?

If insectivorous birds can see UV patterns, then the whole concept of camouflage and cryptic patterns will have to be re-examined. There are many insects which appear to be cryptic to our eyes, but are not cryptic in the UV. If birds can see them, then what was the selection pressure on those insects?

The laboratory results are exciting in themselves, but we still don't know if a bird sees the UV patterns of polarized light in the natural sky. Do they use these patterns for navigation – are they capable of behaving like honeybees?

Atmospheric pressure and infrasounds

It is clear from excellent studies about bird migration and weather patterns that birds are competent meteorologists. The correlation of migration with certain weather patterns is good enough to issue aircraft warnings forcasting high bird densities. We do not know how the birds sense changing weather patterns, we only know that, somehow, they are able to do it.



Figure 4. Acoustic monitors – the four circles – detect and track infrasounds produced by a thunderstorm (square). Data from the U.S. Weather Service. Modified from Bowman & Bedard, 1971.

Meteorologists rely heavily on the barometer as an instrument for detecting weather patterns and their corresponding air pressure changes. Several years ago, I tested homing pigeons in the laboratory for their ability to detect air pressure changes. The birds turned out to be much more sensitive than I had anticipated. They could detect air pressure changes of less than 0.1 mm Hg (Kreithen, 1974a). These were early tests and we had much to learn. But it was clear that the birds had highly sensitive pressure sensors, although we still do not know where this apparatus is located within the bird.

Meteorologists told us of another method for storm and weather detection based on instruments which measure very low frequency sounds (infrasounds) produced by weather and other geophysical events. Infrasounds from storms and other natural phenomena are useful to meteorologists because the sounds are loud (often greater than 100 dB sound pressure level) and because the sounds propagate far and can still be detected even thousands of km from their sources (Figure 4). Besides weather patterns, there are many other natural and man-made sources of infrasounds including: mountains and valleys with appropriate winds blowing (Fig. 5), Aurora Borealis and magnetic storms, earthquakes, ocean waves, volcanoes, jet streams, meteor showers, rocket launches, supersonic aircraft (SST's) and explosions, to name only a few (COOK, 1969; PROCUNIER, 1971; WILSON, 1971; BOWMAN & BEDARD, 1971; BALACHANDRAN et al., 1977).

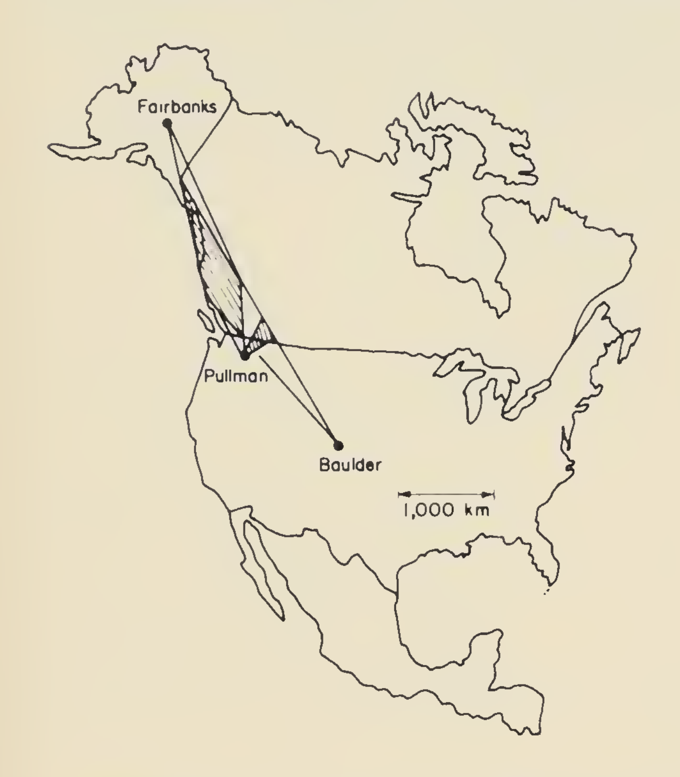


FIGURE 5. Infrasound production by mountains and winds in the Northwestern U.S. Hatched areas are sound producing regions monitored by infrasound microphone arrays (circles).

Infrasounds are sounds of less than 10 Hz and are named to reflect our own inability to hear them. They are true sounds, however, in the sense that they obey the normal laws for sound propagation. Sound attenuation, for example, is proportional to the square of the frequency, and therefore very low frequency sounds can travel extremly long distances with little reduction in amplitude. Some of the infrasounds from volcano eruptions have been observed to circle the globe several times before the energy was dissipated.

We tested homing pigeons in an infrasound chamber in my laboratory, and much to our surprise the birds could detect these extremely low frequency sounds (YODLOWSKI et al., 1977, KREITHEN & QUINE, 1979). Once again, cardiac conditioning methods were used. To summarize the results of several long series of tests, the birds can detect the lowest frequency sounds which we can produce – 0.05 Hz. They are much more sensitive than we are; at least 50 dB better where the ranges overlap at all (Fig. 6). And they detect these sounds with an unknown sense organ that seems to be located within the inner ear structures.

These are laboratory tests, carefully controlled for artifacts. These tests do not prove that pigeons can use infrasounds in the complex world outside of the laboratory. It does not tell us if birds can separate one sound from the many arriving concurrently, or if they

can filter the true infrasound signals from the non-propagating turbulence patterns which sometimes appear with high winds (pseudosounds). Nor do these tests answer how a bird might localize a 0.1 Hz sound where the wavelength is 3.4 km and ordinary binaural localization methods do not work. But it is a good first step, and it does show it is feasible to continue and to explore the possibilities of infrasound cues by birds. There are, of course, many unanswered questions raised by these findings.

How do birds use their pressure sensitivity? Do they use it as an altimeter? It is known that birds do control their altitude even when clouds and darkness obscure visible landmarks (Griffin, 1972). Do they use their pressure sensors as a barometer? Is this what migratory birds use to trigger "Zugunruhe"? Remember – only pigeons have been tested; what about all of the migratory birds? Are infrasounds part of an acoustic map system wherein the bird keeps track of its position with respect to local and long distance sound sources? Can birds hear the infrasounds from approaching storm fronts and are they able to estimate the distance and direction of the storm? I do not know the answers to any of these questions.

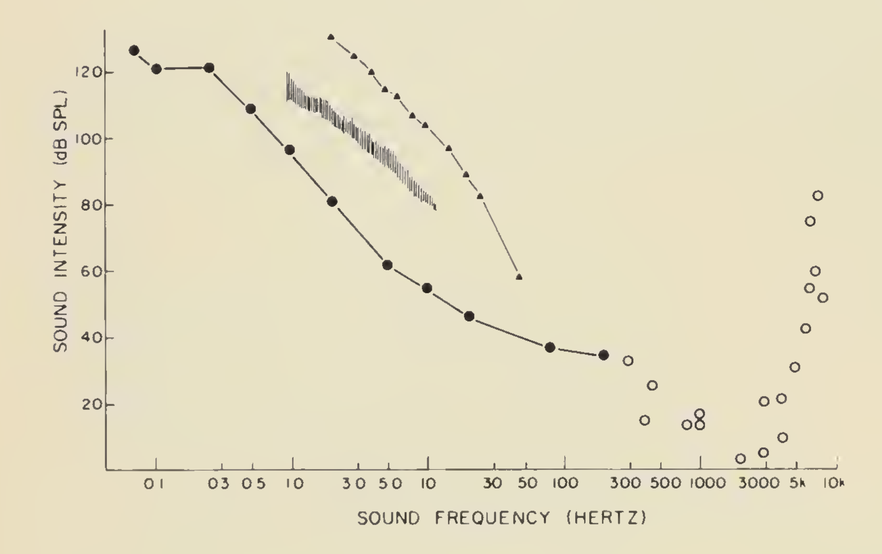


Figure 6. Infrasound sensivity of the homing pigeon. Each filled circle is the result of laboratory testing for infrasound thresholds (50%) determined at each frequency tested. Triangles represent human thresholds and circles are pigeon auditory thresholds by other workers. Vertical bars indicate some natural infrasound levels.

Conclusions

I have asked some simple questions about the senses of birds and I have gotten back some amazing answers from the animals themselves. The birds have indicated that they can detect ultraviolet light, polarized light, atmospheric pressure, and infrasound. I have also performed tests with magnetic fields, olfaction, but space and time limits my discussion of these topics (Kreithen & Keeton, 1974c; Kreithen, 1978a; Keeton, Kreithen & Hermayer, 1977).

These simple laboratory results have raised far more new questions than they have answered. Do the birds use all these sensory channels in their everyday world? Can other birds, not just homing pigeons, do these fantastic things? What else can they do that we haven't even thought to ask? We have seen only the beginning of a long and complex story.

Acknowledgement

The research reported in this paper was supported by grants from the U.S. National Science Foundation.

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Effects of Magnetic Fields on Pigeon Orientation

CHARLES WALCOTT

Since KEETON (1971) showed that homing pigeons with bar magnets on their backs were often disoriented when released under overcast skies, there has been increasing evidence that magnetic fields influence pigeon orientation. It now seems clear that both magnets and Helmholtz coils have a clear effect on the pigeons' vanishing bearings under overcast (KEETON, 1971, 1972; WALCOTT & GREEN, 1974; VISALBERGHI & ALLEVA, personal communication). These results led to the idea that pigeons might use the earth's magnetic field as a compass when the sun was not visible. KEETON & GOBERT's (1970) demonstration that first flight young pigeons had random vanishing bearings under overcast and were disoriented by magnets even under sunny conditions suggested that they were using both the magnetic and sun compass. But even experienced birds that are well oriented under overcast and when the sun is visible use the sun compass, appear to be effected by magnets and Helmholtz coils even under sunny conditions (KEETON, 1972; WALCOTT, 1977; VISALBERGHI & ALLEVA, personal communication). The effect of the magnetic field is much smaller under sunny than in overcast conditions. Under sun, there is usually only a small increase in the scatter of the vanishing bearings or a few degrees difference in the average vanishing direction of pigeons with different polarity Helmholtz coils. The slightness of the effect makes one wonder whether it is real or whether it might be some kind of experimental artifact. That the effect is real is suggested by another series of observations: YEAGLEY (1951), KEETON, LARKIN & WINDSOR (1974), and SCHREIBER & ROSSI (1976) have shown that there is a correlation between sun spot number, the natural variability of the earth's magnetic field and the pigeons' vanishing bearings under sunny skies. ARSETTI (1952), GRAUE (1965), TALKINGTON, (1967), WAGNER (1976), FREI & WAGNER (1976) and WALCOTT (1978) report that anomalies in the earth's magnetic field disrupt the pigeons's initial vanishing bearings. Since magnetic anomalies unlike other fluctuations in the earth's magnetic field are both constant from day to day and fixed in their geographic location, one can compare the degree to which orientation is disrupted with the magnetic topography of the release site. In particular one can see whether there is a relationship between the strength of the anomaly and the amount of disorientation and one can also ask whether there is a correlation between geographic features of the anomaly and the pigeons' orientation. Our hope was that such a comparison might tell us something about the relationship between the magnetic field and the pigeon's orientation.

Procedures

Magnetic anomalies were found using the aeromagnetic maps published by the U.S. Geological Survey. Experienced homing pigeons were released under sunny skies and radio tracked at each site. The compass bearing of the pigeon was recorded every minute until the radio signal disappeared and the direction in which the radio signal was last heard is the vanishing bearing. In addition, data from release points which had been used for other experiments and whose magnetic topography is known are included. For details of the procedure see WALCOTT (1978).

Department of Biology, State University of New York, Stony Brook, New York, USA.

TABLE 1. Correlation between different measures of the magnetic topography and the length of the mean vector of the pigeon's vanishing bearings at twelve different release sites.

	Correlation coefficient
Total magnetic intensity	–.71
0.5 km toward home	–.89
1 km toward home	–.92
2 km toward home	–.80
1 km away from home	–.75
1 km left of home	–.75
1 km right of home	–.74

Results

At the strongest magnetic anomalies, pigeons appear to vanish randomly. But at weak anomalies, there is only an increase in the scatter of the vanishing bearings. Plotting the length of the mean vector, which is a measure of the scatter of the vanishing bearings, against the relative total magnetic intensity at the release site gives the result shown in Fig. 1. Clearly one's subjective impression is confirmed, there is a relationship between the strength of the anomaly and the scatter of the vanishing bearings. Despite this correlation, it could be that it is not the total magnetic intensity at the release site that is important to the pigeon but rather the changes in the magnetic field that the pigeon experiences as it flies in the region of the anomaly. By and large the strongest anomalies have the most irregular magnetic fields, and thus even if it were the variability in the magnetic topography that was important, there might well still be a correlation with the total magnetic intensity. To see if the topography was important we first had to find a way of quantifying the magnetic irregularity at each anomaly. Generally we have chosen the release sites so that pigeons are released at the point of greatest magnetic intensity at each anomaly. Thus whichever way a pigeon flies it will experience a decrease in total magnetic intensity. We have chosen to measure this decrease along a line of a given length in a given direction. Thus the number given for magnetic variability is the difference between the field strength at the release

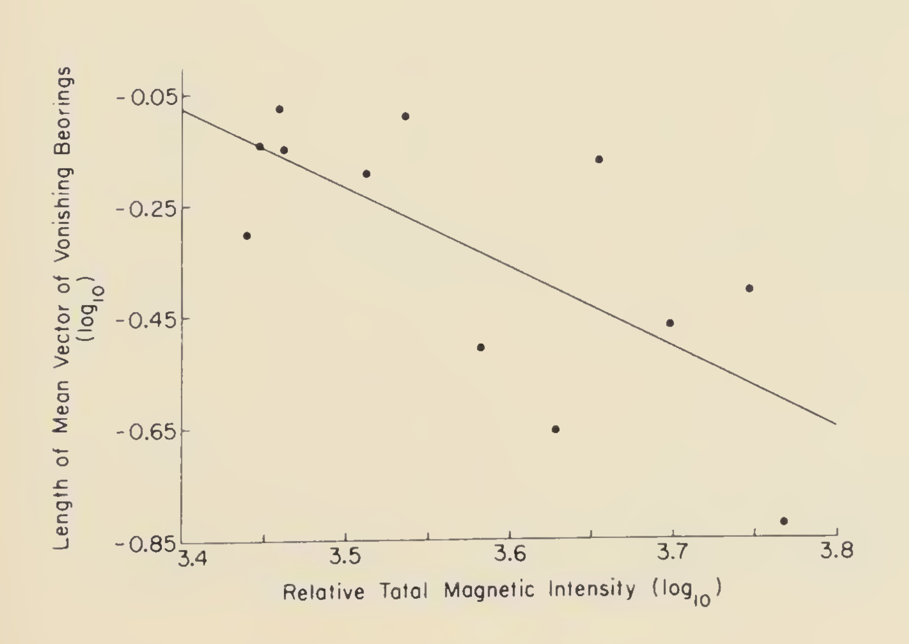


FIGURE 1. The total magnetic intensity, in gammas, is plotted against the length of the mean vector of the pigeons' vanishing bearings for each of the twelve release points. The magnetic intensity data were taken from the U. S. Geological Survey Aeromagnetic Survey maps and are given relative to some arbitrary and unstated datum. Each point on the graph represents the mean vanishing bearings of 15 to 54 birds released for the first time at each site. The solid line is the regression line plotted by the least squares method.

point and the lowest field strength anywhere along the line. We have tried to correlate the magnet variability along various length lines in different directions from the release points with the scatter of the pigeons' vanishing bearings; some examples are shown in Table 1. Figures 2 and 3 show two of the most interesting relationships: the length of the mean vector plotted against the magnetic variability along a 1 km line towards and away from the home loft. All the corelations between the magnetic variability and the scatter of the vanishing bearings of the pigeon are significant at the value of $p = 0.05$ or less. But the best correlation is with the magnetic topography along a 1 km line toward the loft. Unfortunately this correlation is not significantly better than any of the others; there are not enough data.

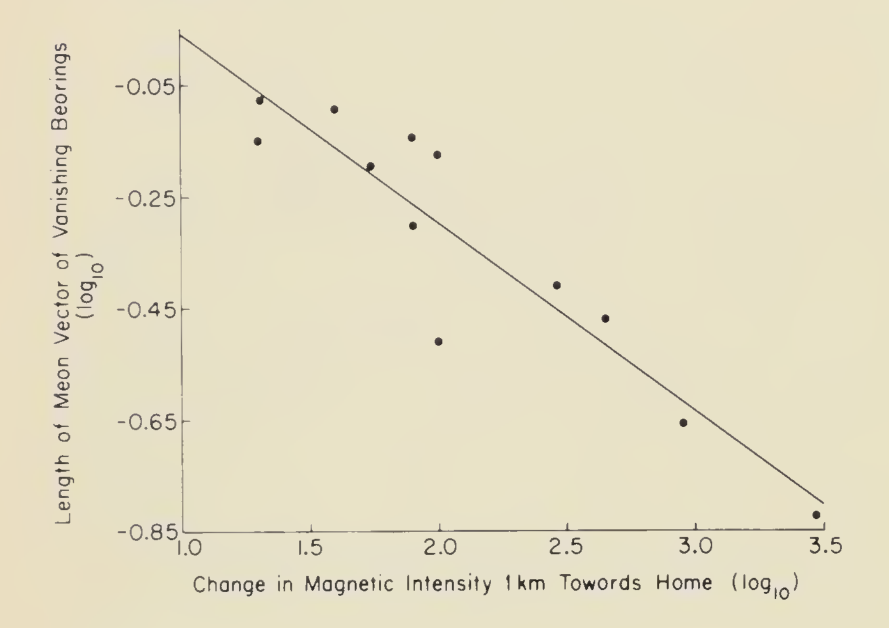


FIGURE 2. The maximum change in magnetic intensity, in gammas, from the release site along a 1 km line oriented towards the home loft is plotted against the length of the mean vector of the pigeons' vanishing bearings at each site. These are the same data from the same release sites as shown in Figures 1 and 3.

Discussion

The major point that emerges from this and the other studies of YEAGLEY (1951), WAGNER (1976) and SCHREIBER & ROSSI (1976) is that variability in the earth's magnetic field has an effect on pigeon vanishing bearings even under sunny conditions. This result clearly implies that the idea that pigeons switch between a magnetic and a sun compass depending on whether the sun was visible or not was too simplistic. The earth's magnetic field seems to play some role in orientation even when the sun is visible.

Two obvious possibilities are that either there is some form of interaction between the two compass systems or that the magnetic field is involved in the pigeon's navigation or map. The question of whether the scatter of the pigeons' vanishing bearings is best correlated with the magnetic topography in the homeward direction is obviously crucially important in deciding between these two alternatives. If further releases at other anomalies and from various directions around the anomaly show that the magnetic field toward home is the most important, this certainly suggests that pigeons somehow know the correct direction toward home despite the magnetic disturbance. It would imply that the irregular magnetic field at the anomaly was disrupting a compass system rather than interfering with the pigeon's navigation or map. But even if this proves to be the case the results are very interesting: how could a disturbance of the magnetic field intefere with the operation of the sun compass? Young first flight pigeons apparently require both the sun and the earth's magnetic field for accurate homeward orientation (KEETON & GOBERT, 1970). Perhaps

some sort of cross check between the two compass systems is present even in adult birds. But this seems unlikely for a number of reasons. First, clock shifts cause a predictable deviation in the initial headings. Second, Helmholtz coils which cause a major shift in vanishing bearings under overcast have a much smaller effect under sun. It could be argued that in this case the pigeons were relying exclusively on the sun compass, but if that were the case, why wouldn't they do the same thing at magnetic anomalies? The general conclusion that I come to is that there is no clear explanation of what the relation is between the two compass systems.

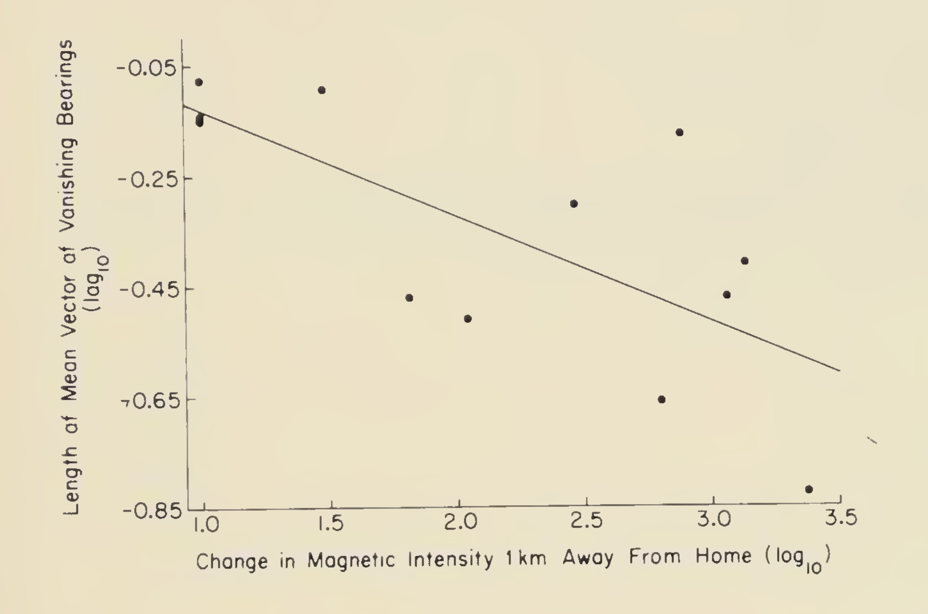


FIGURE 3. The same procedure as in Figure 2, but the line was oriented away from the home loft.

LINDAUER (personal communication) has shown that honey bees in essentially constant conditions can use the daily fluctuations in earth's magnetic field to entrain their biological clock. Even if this were true of pigeons, the birds used in our releases have a clear view of the sun and natural day at the loft before being taken to the release site. They are certainly not deprived of photoperiod information as LINDAUER's bees were.

A final possibility is that the variability of the Earth's magnetic field disturbs the pigeon in some non-specific way. Perhaps it interferes with the operation of some other sense organ. This seems unlikely because strong, earth strength, magnetic fields attached directly to the pigeon have a small effect, while the very small normal fluctuations in the earth's field do alter orientation. It seems most unlikely that these small 10–100 gamma fluctuations would cause a general disturbance in any sense organ. The only conclusion that seems to me safe, is that magnetic fields do have an effect on pigeon vanishing bearings even under sunny conditions. But how that effect occurs is unclear. Perhaps a further exploration of pigeon orientation at and around magnetic anomalies may give us a hint of what role the earth's magnetic field plays in pigeon orientation.

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The Importance of Outward Journey Information in the Process of Pigeon Homing

J. Kiepenheuer

Evidence is accumulating that information picked up en route is used in the navigational process of the pigeon. Detours (Papi et al. 1973, 1978, Hartwick et al. 1978), inversion of the vertical – (Kiepenheuer 1978 a, b) and of the horizontal magnetic field during transport (Wiltschko et al. 1978 a, b) and transporting the birds in iron boxes (Papi et al. 1978) influence the orientation behavior. To evaluate these results we have to consider that there are 3 sorts of information the bird may derive from the magnetic field: 1) mere compass information 2) information on the magnetic landscape (dip angle and intensity) and 3) possibly information derived from moving through the field. Transport in artificially reversed fields affects only the compass information en route, while carrying the birds in closed iron boxes deprives them of any information concerning the magnetic field. Since all procedures result in a "wrong" orientation on release as demonstrated by the vanishing bearings, we have to investigate step by step the mechanisms involved. Passive transport is by no means the natural way of moving around for a pigeon. In flying the heading of the bird approximately coincides with its track; any differences between track and heading are due to lateral drift by wind. Passive transport may be viewed as a sort of drift which the bird has to perceive in some way. A compass alone, without any other (e. g. optical) reference system, will not furnish this information. It gives only information on changes in the heading during transport – this information may under normal conditions be the most important one.

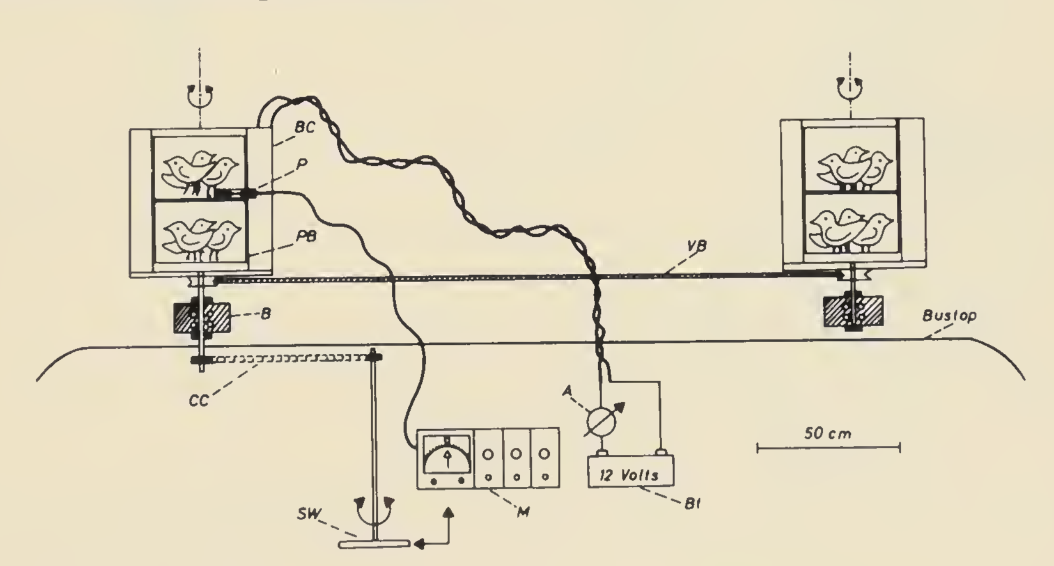


Figure 1. Experimental setup for keeping the pigeon boxes (PB) aligned with respect to magnetic north and for reversing the field during transport. BC = boxcoil, P = magnetometerprobe, M = magnetometer, B = bearing, CC = cog and chain, VB = V-belt, SW = steering wheel, Bt = battery, A = ampère- and potentiometer.

One purpose of the experiments reported here was to block the information on changes in the heading by keeping the transport boxes and the pigeons therein constantly aligned

Abt. f. Verhaltensphysiologie, Universität Tübingen, Bundesrepublik Deutschland.

with respect to magnetic north, the other aim was to reverse the direction of the horizontal magnetic field during transport. The experimental setup is illustrated in Fig. 1. The pigeons (up to 16) are carried in double storied closed boxes (PB) ventilated by cloth covered holes, surrounded by cubic box coils. The box coils (RUBENS 1945) are used to generate a homogenous horizontal magnetic field inside the pigeon boxes. In this experiment the field strength was so adjusted that together with the earth field it resulted in a magnetic field exactly opposed to the natural field but of the same magnitude and dip. Two pigeon boxes with coils are mounted on turntables on top of our VW bus, connected by a V-belt. The axis of the front turntable enters the bus and is connected to a steering wheel by a cog and chain mechanism. So both boxes can be turned simultaneously from inside the bus. Inside the front box a magnetometer probe (P) is mounted horizontally, perpendicular to the field of the box coil. The probe is connected to a magnetometer inside the bus. By turning the wheel by hand the probe is so adjusted that the magnetometer on a sensitive range reads zero, meaning exact E-W alignment. Any small deviation from this alignment with respect to magnetic E-W immediately results in a large reading of the magnetometer. By turning the wheel and keeping the magnetometer reading zero the boxes are kept aligned almost perfectly with respect to magnetic north during transport to the release site. Maximum short time deviations under severe conditions (very bumpy road or abrupt turns) were on the order of ± 10°, while normally the alignment was perfect within about ± 2°.



FIGURE 2. Release sites and transport routes. L = loft, O = upto 25 km, ● = 25–70 km.

Deviations caused by passing trucks or iron structures often were considerably larger. In most experiments three groups of pigeons were used. One group was carried in a turntable box with the magnetic field reversed, turned on ca. 200 m from the loft and turned off on arrival at the release site, (E-birds), one group in a turntable box in the natural field (C-birds) and one group in a cloth covered crate fixed to the roof (SC-birds). The treatment was rotated among the groups from one experiment to the next, so all pigeons were treated alike. The experiments were carried out from May to November 1977. Young

birds (fall 76/spring 77) were used, beginning with short range releases and gradually longer range releases up to 70 km (see Fig. 2 for tracks and release sites). The birds were released alternately one by one and tracked in the usual manner by 7x50 binoculars until out of sight (ca. 1.5–2 km). Vanishing bearings, vanishing times and homing speed were recorded.

Treatment of data

Vanishing bearings were treated according to standard methods of circular statistics (BATSCHELET 1965, 1972; MARDIA 1972). The nonparametric WATSON U^2 test normally used in comparing directional data is insensitive to bimodal distributions, so I was forced to use a less sensitive X^2-test on most of the data (comparing the number of birds vanishing in the homeward and the opposite semicircle). The bearings were tested for circular normal distribution by the KUIPER-KOLMOGOROW test, when bimodal by doubling the angles. Vanishing times were compared by the nonparametric MANN-WHITNEY U-test and, since the logarithmic data are almost normally distributed these were tested by the t-test in pooled data of several releases after normalizing the data to the mean of all data of the day concerned. Differences in homing speeds between groups were compared by the MANN-WHITNEY U-test.

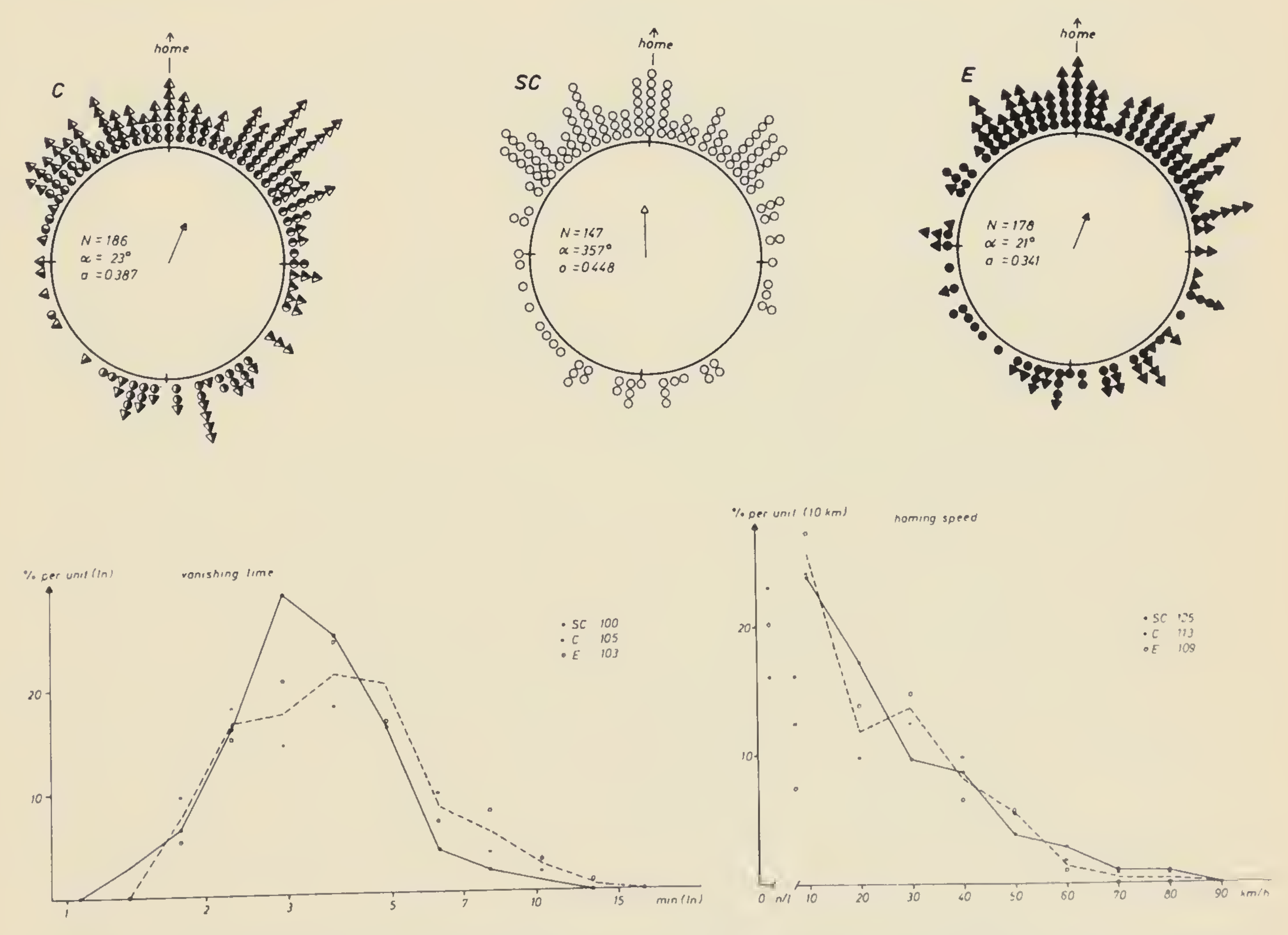


FIGURE 3. a) Vanishing bearings of pigeons from sites up to 25 km from the loft carried on turntables (E = experimentals with magnetic field reversed, C = controls) and carried fixed to the roof (SC = supercontrols). The arrow denotes direction (α) and mean vector -length (a) of the bearings. Triangles stand for releases carried out without supercontrols. b) Distribution of vanishing times on a logarithmic scale (left) and homing speeds (right).

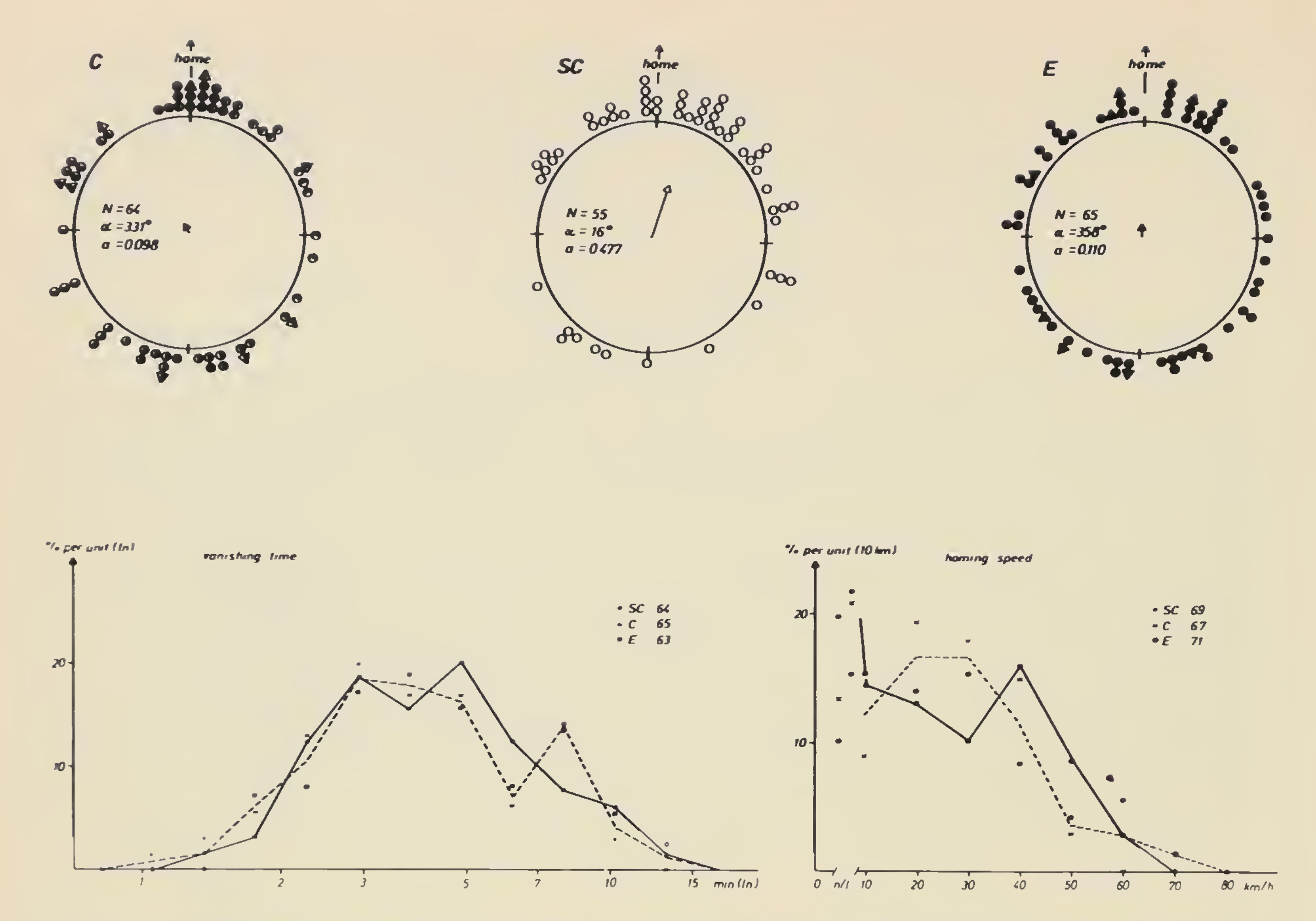


FIGURE 4. Vanishing bearings (a) and vanishing times and homing speeds from release sites 25–70 km from the loft (see Fig. 3).

Results

In order to condense the data they were pooled in two groups (release sites up to 25 km and 25–70 km from the loft) even though some individual experiments yielded significant results. Fig. 3a shows the vanishing bearings of 17 releases from 9 sites (see Fig. 2) up to 25 km from the loft. SC are supercontrols carried fixed on the roof, E are birds carried on turntables with the magnetic field reversed, C are birds carried on turntables in the natural field. The mean vectors of all three groups are homeward oriented (V-test). The C and E birds both show a bias to the right of the supercontrols ($p < 0.05$; WATSON & WILLIAMS test). Applying the X^2-test on the data reveals no significant difference between C and E ($p = 0.6$) nor between C plus E and SC ($p = 0.28$) concerning their tendency to fly away from home on release; the distributions do not differ significantly from circular normal. Fig. 3b shows the vanishing times and homing speeds of the birds released at short range. Vanishing times of C and E birds are significantly longer than those of the supercontrols ($p = 0.05$, $p = 0.02$, respectively C and E combined are significant at $p < 0.001$ – t-test on logarithmic data). The difference in vanishing times between C and E birds is not significant. Homing speeds of all three groups at short range releases are virtually the same. Fig. 4a shows the pooled vanishing bearings of 8 releases from 8 different sites 25–70 km from the loft (Fig. 2). There again is no significant difference in the behavior of C and E pigeons ($p = 0.95$). The behavior of SC birds, compared to the E and C birds, though, is obviously very different. The X^2-test (one sided) shows that E as well as C birds tend to head off in the direction opposite of home ($p = 0.025$, $p = 0.008$ resp., combined $p = 0.006$).

The triangles stand for bearings obtained in experiments without supercontrols (SC); these data were only used when comparing the behavior of C and E birds. A detailed analysis of the data showed that the bearings of C and E birds actually are bimodally distributed (after doubling the angles the mean vector becomes longer, applying the Kuiper-Kolmogorow test reveals the data to be normally distributed. The distribution of SC bearings on the other hand is not different from a unimodal normal distribution. (More details will be given in a future publication.) At longer range (25–70 km) vanishing times in the three groups are about the same (C and E combined 4.03 ± 0.2, SC 4.16 ± 0.2 minutes, x, sx). Homing speeds of SC are slightly higher than those of the C and E birds (Mann-Whitney U-test, $p=0.16$). When we consider only the faster 50% of every group (assuming that these actually were eager to home) and of these again only those birds which headed off outside ± 60° of the home direction the difference in homing speed between SC ($n = 17$) and C + E birds ($n = 40$) is highly significant ($p = 0.0015$) (see Fig. 4b, c). The difference in the number of birds vanishing in the direction opposite of home between short range releases (up to 25 km) and long range releases (25–70 km) is significant at a level of $p = .04$ for the E-birds, $p = .01$ for the C-birds and $p < .001$ for E plus C combined, while the supercontrols (SC) show absolutely no difference ($p = 0.95$).

Discussion

Depriving pigeons of information on the turns encountered during transport obviously has an influence on their navigational behavior. Navigational mechanisms based on this sort of information have often been discussed e. g. by Barlow (1964). Manipulation of the sensory systems possibly involved has been unsuccessfully attempted, e. g. by partly destroying the vestibular apparatus (Wallraff 1965, Exner 1893), spinning the birds during transport (Matthews 1951) or anaesthetizing them (Walcott & Schmidt-Koenig 1973). The results presented here prove that the navigatory mechanisms of the pigeon actually do utilize information on turns during transport. At short range other mechanisms (e. g. orientation by air borne information) may obscure the effect, so deprivation of "turn information" may result only in a bias to the right similarly observed at short range when transported in a reversed magnetic field (see Kiepenheuer 1978 a, b) and in longer vanishing times, suggesting that the bird is in some conflict about the information concerning the location of the site. At longer range the assumed "short range information" seems to decrease; pigeons deprived of "turn information" do not hesitate to fly off; vanishing times equal those of controls; but the pigeons obviously are incapable of differentiating between the home course and the opposite direction. If this is so, it is not surprising that the pigeons transported on turntables in a reversed magnetic field show no different behavior than those carried in the natural field. Pigeons carried on turntables and heading off in a wrong direction home significantly slower than controls flying off in the wrong direction. In the end most of the experimental pigeons home. I therefore assume that at a range of up to at least 70 km pigeons are able to obtain enough other – e. g. air borne – information to decide whether the direction chosen is right or wrong, given enough time to acquire this information. This might carry them out of sight of the observer. With growing distance from the loft pigeons kept aligned with respect to north more often head towards the wrong direction. The pattern of decrease of this – maybe olfactory – information available to the pigeon is gradual, presumably logarithmic, but

many more experiments are necessary to establish the exact pattern. Information derived from being carried through the magnetic field on the other hand might improve approximately linearly with distance. The two sets of information would necessarily lead to a minimum of information at some distance from home. According to experiments carried out so far, this seems to be the case at about 30–40 km. This again corresponds well with the results of SCHMIDT-KOENIG (1966, 1968). I have no definite answer yet to the question as to why the orientation of pigeons deprived of turn information en route is bimodal. The effect, though, points to the possibility that the navigational information available to the pigeon on release includes at least two components; one informing the bird about the orientation axis home – away from home; the other telling it which of the two directions is right. The latter seems to be affected by depriving the bird of turn information during transport, possibly by fooling it about the distance of transport. The analysis of this behavior and other considerations lead to a hypothesis of navigation to be presented in a future paper.

Acknowledgements

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The Development of Sun Compass Orientation in Young Homing Pigeons

ROSWITHA WILTSCHKO

Introduction

Although homing pigeons are very well able to orient when the sun is not visible (KEETON 1969), phase shifting their internal clock regularly results in departure bearings deviating from those of control birds according to the amount of phase shift and whether the shift was fast or slow (e.g. SCHMIDT-KOENIG 1961; see KEETON 1974 for review). This clearly demonstrates the outstanding role of the sun compass in homing: whenever the sun is visible, the sun compass is preferentially used, dominating over all other systems not undergoing a periodical change.

Very little, however, has been known about the ontogeny of this prominent orientation system. Using the sun compass requires the birds to know the relationship between their internal clocks, sun azimuth and geographic direction. How is this relationship formed? Here we will sum up the results of two test series which give some indications how the sun compass develops in young homing pigeons.

The sun compass – innate or established by experience?

The question was: is the sun compass in birds inherited or is it learned by experience? To answer this question, the experience of young pigeons had to be manipulated presenting them a false yet non-contradictory relationship of time, sun azimuth and direction. The easiest way to achieve this was to manipulate the birds' internal clocks.

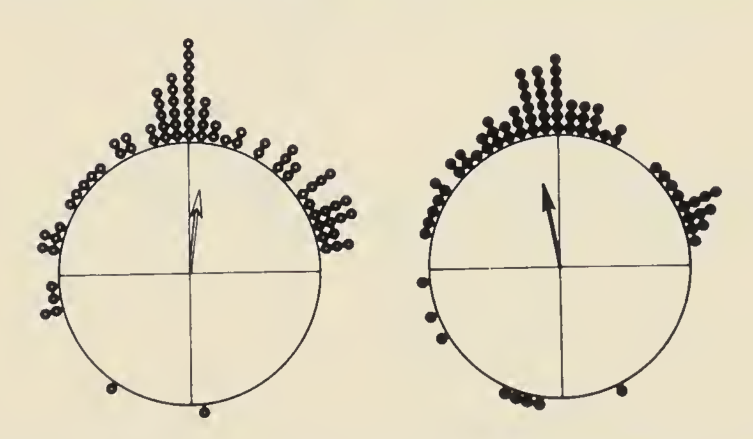


FIGURE 1. The pooled departure bearings of 7 releases of "permanently" slow shifted pigeons (solid symbols) do not differ from the corresponding bearings of controls (open symbols). In this and all later figures, the mean vectors are shown as arrows whose lengths are drawn proportional to the radius of the circle = 1. Unless stated otherwise, home is set equal to 360°.

Two groups of young pigeons were housed from their weaning age onward in two adjacent light-tight rooms. For the control group, the photoperiod matched the natural photoperiod outside; for the experimental group, the photoperiod was set 6 h slow, i.e. the lights came on 6 h after sunrise and went off 6 h after sunset, causing these birds to grow up and live under a permanent 6 h slow clock shift. During the overlap time of the

Fachbereich Biologie der Universität, Zoologie, AK P. Ö. V., Siesmayerstraße 70, D 6000 Frankfurt, Bundesrepublik Deutschland

natural and the artificial photoperiods in the afternoon, both groups were released together for exercise flights around the loft and later for a series of flock training releases up to about 35 km from the cardinal compass directions. Thus both groups of young pigeons had abundant opportunity to see the sun during their post-weaning development, but all their experience took place in the afternoon, which was the subjective "morning" for the experimental birds. For details of the experimental procedure, see WILTSCHKO et al. (1976).

When these pigeons were released singly under sun in the usual manner, the orientation of the permanently slow-shifted birds did not differ from that of the controls. Fig. 1 gives the pooled departure bearings of 7 such releases from different sites. In none of these tests was a difference in vanishing interval, homing success, or homing speed found.

Thus the permanently slow-shifted birds showed no indication of the altered orientation behavior normally observed in pigeons whose internal clocks had undergone a regular clock shift by exposure to an altered photoperiod for a few days. Their orientation system appeared to function correctly in spite of the abnormal experimental situation. It was not clear yet, however, whether the permanently slow-shifted pigeons used a sun compass at all or whether they relied exclusively on not periodically changing mechanisms such as the magnetic compass (cp. KEETON 1971; WALLCOTT & GREEN 1974). This was to be decided by a "regular" clock shift of the experimental birds back to normal time.

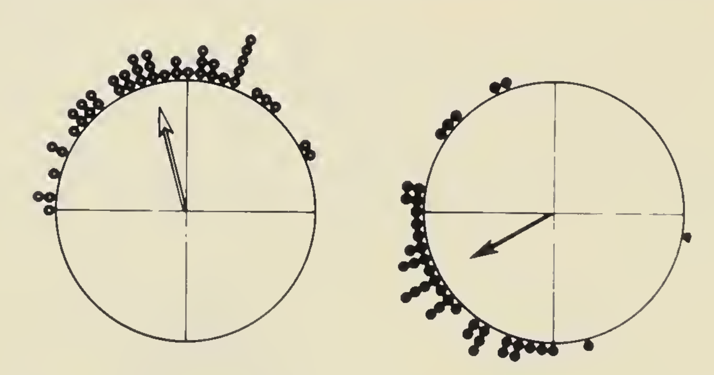


FIGURE 2. The pooled departure bearings of 4 releases of former permanently 6 hour slow shifted pigeons on their first flight after normalization (solid symbols) show a significant 104° counterclockwise deviation from those of the controls (open symbols).

Fig. 2 gives the pooled departure bearings of 4 releases where former permanently shifted birds flew for the first time under sun after being normalized. The bearings of the experimental birds show a significant ($p < 0.001$, WATSON WILLIAMS Test) counterclockwise deflection (ca. 90°) from those of the controls. Thus the normalized birds reacted like 6 h fast-shifted birds, (cp. Fig. 3) i.e. they reacted to the phase shift of their photoperiod and not to the absolute position of the light phase within the day.

These data clearly show that the pigeons living under a permanent clock shift were using a sun compass. But their sun compass was different from the sun compass of normal birds: it had been adapted to the experimentally set up situation by reading the morning sun as a southerly sun, etc. So we conclude that the pigeons' sun compass is not inherited, but must be established by individual experience.

Later experiments indicated that the sun compass of the former permanently shifted birds could be readjusted to the natural situation to some extent (see WILTSCHKO et al. 1976).

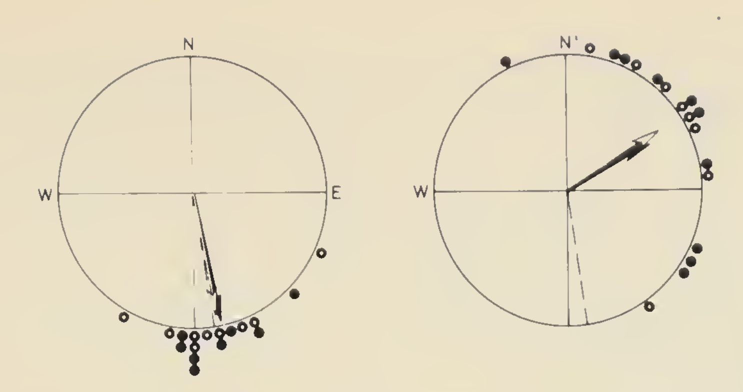


FIGURE 3. Data of an experiment comparing four different groups of pigeons. The home direction, 172° S, is marked by a dashed line; home distance: 74 km.
(a) The departure bearings of the "permanently" slow shifted pigeons (solid symbols) and the untreated controls (open symbols) are homeward oriented and almost identical.
(b) The departure bearings of the "normalized", formerly "permanently" 6 hour slow shifted pigeons (solid symbols) are distributed like the bearings of 6 hour fast shifted pigeons of the control group (open symbols), their means deviating 109° and 112°, respectively, from the mean of the untreated controls and the "permanently" shifted birds.

When is the sun compass established?

When the sun compass was shown to be established by experience, the circumstances of this learning process became of interest. At what age do pigeons possess a fully developed sun compass? A series of clock-shift tests with young pigeons was to answer this question.

We used first-flight birds, i.e. pigeons that had never been taken away for training releases prior to the critical test. They had been allowed daily exercise flights around their loft, and for the tests, they were confined in light-tight rooms for at least five days, setting the internal clocks of the experimental birds 6 h fast. To check the test performance, a group of young trained pigeons was subjected to the same procedure.

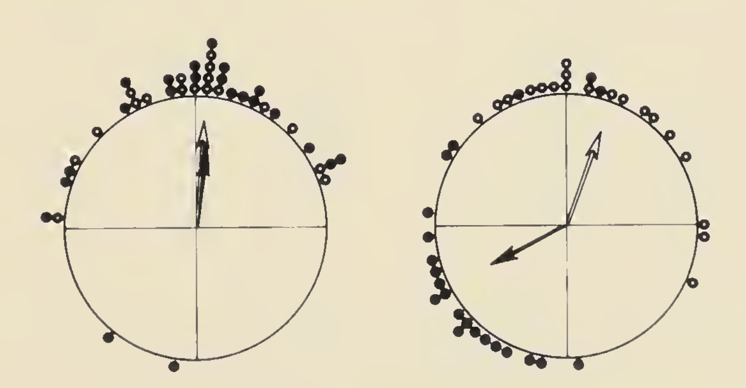


FIGURE 4. (a) The departure bearings of 6 h fast shifted first-flight pigeons, 9 to 10 weeks of age, are homeward oriented like those of untreated first-flight birds.
(b) In the trained controls, the 6 h fast shift resulted in a 136° counterclockwise deviation. (Data from 2 releases pooled)
In this and the following figures, solid symbols indicate bearings of pigeons whose internal clocks had been reset 6 h fast, and open symbols indicate bearings of untreated birds.

The pooled departure bearings of two clock-shift tests with first-flight pigeons 9 to 10 weeks of age are presented in Fig. 4a. The 6 h fast-shifted first-flight birds were homeward oriented like the untreated birds ($p < 0.001$, V-Test to home and the direction of the controls), and the orientation behavior and homing performance of the two groups did not differ in any way. The trained birds, however, showed the ca. 90° counterclockwise

deviation normally observed after a 6 h fast shift (untreated vs. shifted: $p < 0.001$, WATSON WILLIAMS Test, cp. Fig. 4b). Fig. 5a presents corresponding data on two tests with first-flight pigeons about a week older. Here a small deviation in the expected direction was observed, but it is not significant ($p > 0.05$) and by far smaller than the shift observed in the trained controls (Fig. 5b). These findings agree with an observation by KEETON (1971 b) that the effect of clock shift in young first-flight birds is different from that in adult experienced birds.

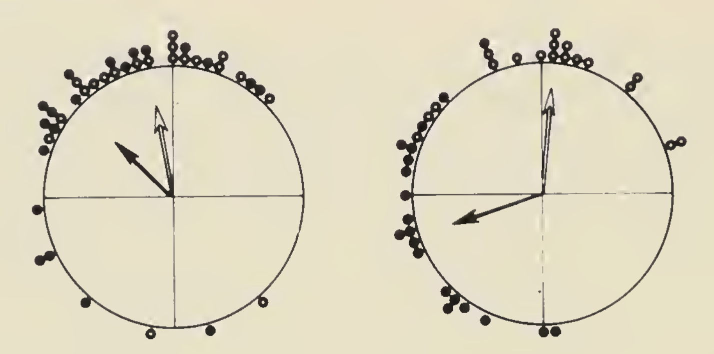


FIGURE 5. (a) The departure bearings of 6 h fast shifted first-flight pigeons, 10 to 11 weeks of age, show a small (-32°), yet not significant deviation in the expected direction from those of the untreated first-flight birds.
(b) In the trained controls, the 6 h fast shift resulted in a 113° counterclockwise deviation. (Data from 2 releases pooled)

A deviation of the expected amount was observed for the first time in pigeons 12 weeks of age (Fig. 6a), and it was regularly found in first-flight pigeons of 16 weeks and older (Fig. 6b).

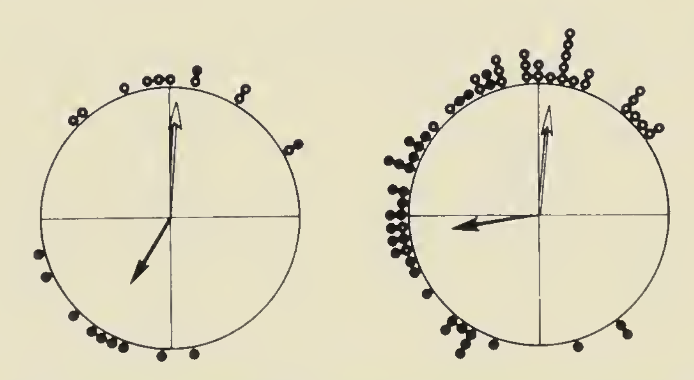


FIGURE 6. (a) In 6 h fast shifted 12 weeks old first flight birds, a significant 151° counterclockwise deviation from the untreated birds was found.
(b) First-flight birds of 16 weeks and older regularly showed the expected deviation when subjected to a 6 h fast clock shift. (Data from 3 releases pooled)

Thus first-flight pigeons less than 10 weeks of age were able to depart homeward oriented and to actually home from distances compatible with their still limited flight perseverance, but they apparently did not utilize the sun for direction finding. Our data show that the sun compass is normally established at about the 12th week of age, soon to take over its role as the predominant compass system.

We want to point out, though, that our data clearly indicate that the ability to home is fully developed before a sun compass is used. Hence determining the home direction and homing appear to be primarily independent from the sun compass. It is not clear what orientation mechanism the very young pigeons are using instead. KEETON'S (1971 a)

observation that young first-flight pigeons were disoriented by magnets glued to their backs even when the sun was visible might be interpreted as suggesting that they utilize information from the geomagnetic field.

Conclusion

Our findings reported here indicate that pigeons at a very young age possess the orientational capabilities to home, based on cues which do not undergo a change in the course of the day. At the age of about 12 weeks, the sun compass is established by a learning process and quasi posteriorily added to the already functioning navigation system, where it then becomes the compass mechanism predominantly used.

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Homing Strategy of Pigeons and Implications for the Analysis of their Initial Orientation

Hans G. Wallraff

It is important to know the environmental cues that are involved in bird navigation, but it is also important to analyse the strategies by which the birds make use of the input data they are gathering. I will discuss certain aspects of these strategies together with methodological consequences which follow from the specific behaviour of displaced pigeons.

Compass orientation versus goal orientation

When dealing with pigeon homing we are dealing with goal orientation. However, not each oriented behaviour of displaced pigeons is necessarily goal-oriented.

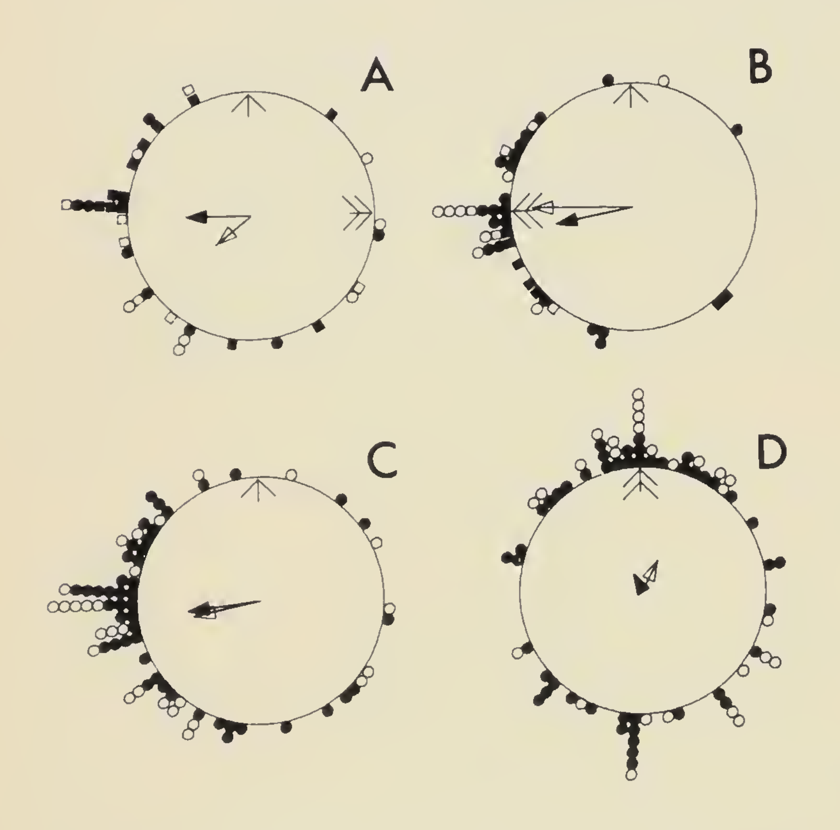


Figure 1. Vanishing bearings of first-flight pigeons from a loft at Seewiesen near Munich. Filled symbols refer to birds whose olfactory nerves were bisected several weeks or days before release, open symbols to untreated or sham-operated controls. A: releases 92 km (squares) and 199 km (circles) west of home; B: two releases (different symbols) 112 km east of home; C: data of A and B pooled with north upward; D: the same with home upward. Respective mean vectors are indicated as arrows, radius of circles corresponding to maximum possible length.

The problem may be illustrated by an example. Fig. 1 B shows initial bearings of inexperienced pigeons about 100 km east of their loft. In one of two groups of birds (black symbols) the olfactory nerves were bisected (cf. Papi 1976). From the diagram one might conclude that olfactory nerve cutting has no or little effect on homeward orientation. Although scatter is slightly increased in the experimental animals, it is, according to the V test (Batschelet 1972), highly significant and beyond any doubt that the operated birds preferred the direction towards home.

When the pigeons were displaced westward, however, both groups pointed, on average, away from home (Fig. 1A). Only the scatter was increased, especially in the controls. Pooling of the two diagrams demonstrates obviously oriented behaviour if north remains

Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, Bundesrepublik Deutschland.

upward (Fig. 1C), but more or less disorientation if the bearings are arranged with the respective homeward direction pointing upward (Fig. 1D).

We certainly can conclude from these data that pigeons deprived of olfaction are clearly oriented. However, I think we can conclude nothing about the effect of olfaction on homeward orientation or goal orientation. Even the controls are so weakly oriented homeward that demonstration of a possible difference would need many more data.

It appears to me that this conclusion is not a matter of course for everybody, especially not for ,,pigeon people" who are accustomed to the fact that the vanishing bearings of pigeons usually deviate somewhat from the direction towards home. In most cases, the deviations are less than 90°, but sometimes they can approach up to 180°. In former times we thought that these ,,release-site biases" commonly reflect distortions or rotations of the so-called map of the pigeons, and this view still seems alive (cf. KRAMER 1959, WALLRAFF 1959, KEETON 1974, 1979). On this basis one may interpret any direction a pigeon chooses as its subjective homeward direction. This would imply that, per definition, all orientation a displaced pigeon performs is goal orientation. Such an hypothesis, however, would corrupt all the terms and definitions we normally use in this field. If Fig. 1A demonstrates goal orientation, then PERDECK'S (1958) juvenile Starlings that were displaced from their normal migration route and continued their course afterward, were also goal-oriented.

I prefer to stay on safe ground by speaking of goal orientation only in such cases in which a geometric relationship to the goal can be proven, since the goal is the only point of reference we have without making specific hypotheses. Goal-oriented behaviour, however, can never be proven by releases at only one site.

It is a methodological consequence of these considerations that one always should do what has been done in the above example (Fig. 1); the same kind of releases should be conducted at several sites symmetrically distributed around the loft, at least at two opposing sites. Only the pooled data can then reveal the degree of homeward orientation, and the V test can be used appropriately only for the combined data.

(Such pooling also has to be done with some care in case unequal numbers per release site are involved. Fig. 1 demontrates how it normally should not be done. There are only 20 blacks dots in A, but 27 in B. Thus, in a simple summation the eastern data are overrepresented as against the western data, and so homeward as well as westward orientation appears stronger than it should be. See WALLRAFF 1979, Appendix B.)

The example shown in Fig. 1 is rather extreme, but it coincides with the general pattern of directions that has been observed in inexperienced pigeons from this loft. Those pigeons commonly prefer westerly or southwesterly directions, and their initial bearings are usually accumulated between this direction and the direction towards home. A preferred compass direction (PCD) like this has been found at each of the eleven home sites that have been investigated systematically (WALLRAFF 1978). The particular direction itself is a loft-specific constant, and it depends mainly on the angular relation between the respective PCD and the homeward direction whether the so-called release-site bias is to the left or to the right of home.

PCDs in pigeons are similar and perhaps identical with a phenomenon that is known from wild birds and that MATTHEWS called ,,nonsense orientation" (GRIFFIN & GOLDSMITH 1955, BELLROSE 1958, MATTHEWS 1961, 1963). Although I accept MATTHEWS' (1961) warning not to interpret everything a displaced pigeon does as goal

orientation, I am not willing to adopt his term ,,nonsense orientation". I prefer to describe the birds' behaviour operationally and speak simply of preferred compass directions. Further, as I assume that the PCDs are necessary outcomes of the bird's homing strategy, I am trying to make sense of them.

Null-axis hypothesis and recent data

In an earlier study (Wallraff 1974) I have discussed in detail how birds might evaluate position-dependent coordinates in order to reach their home from a distant site. The ,,null-axis hypothesis" resulting from these considerations was in good agreement with the empirical data that existed at that time. However, in order to test the hypothesis further and, possibly, to recognize not only main principles, but also concrete components of the system, it appeared necessary to broaden the empirical basis. For this purpose a new loft was established at Würzburg so that all the predictions that had been made are to be tested now in a virgin area. The long-term experimental program is still going on, but some principal trends can be outlined. Fig. 2 may illustrate the hypothesis as well as its coincidence with the initial bearings of inexperienced pigeons of the Würzburg loft.

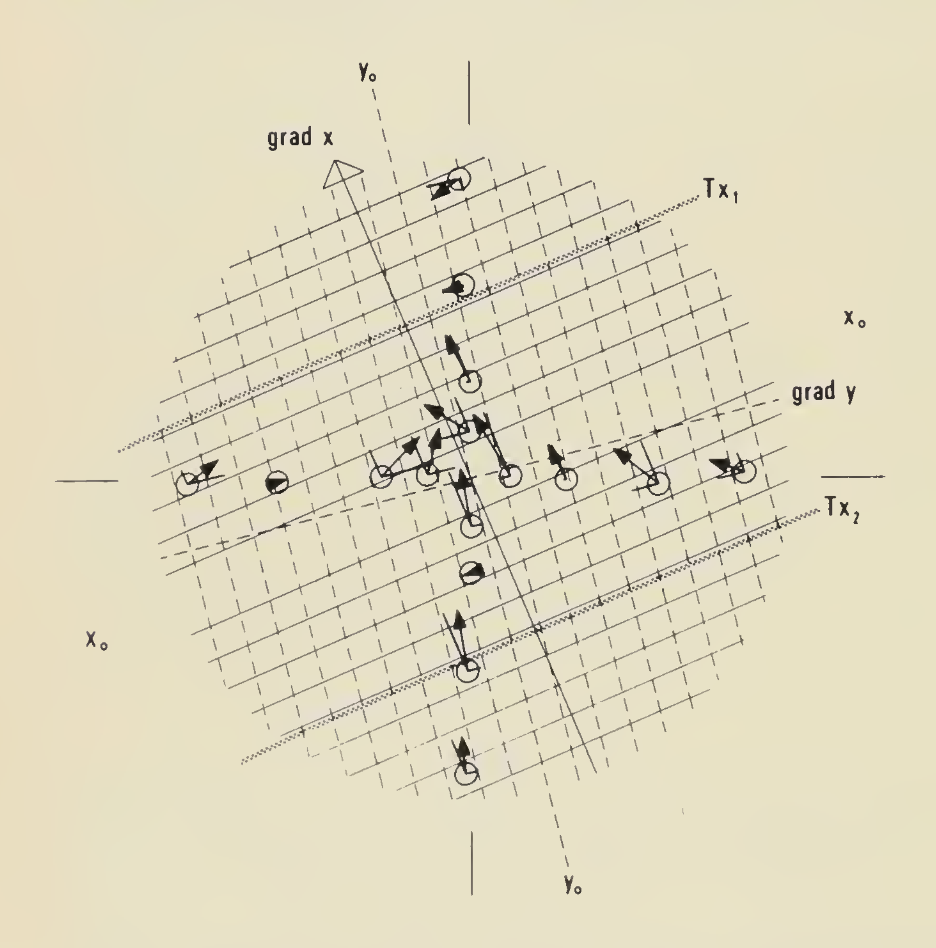


Figure 2. Mean vanishing bearings of first-flight pigeons settled at Würzburg. The field shown has a radius of 200 km with the loft in its centre and with north pointing upward. Each arrow represents the mean vector calculated from 27 bearings (3 releases, 3 years) at distances ca. 30 and 60 km, and from 18 bearings (2 releases, 2 years) at distances ca. 120 and 180 km. Small circles correspond to vector length $\bar{a} = 0.1$. Further explanation in the text.

The hypothesis is based on the assumption that a homing bird makes use of at least two coordinates or gradient fields, whatever they physically may be. The bird may be able to store the respective values, x_o and y_o, measured at home. The two values shall exist along two lines running through home and intersecting at an angle that must not be too small. Displaced to a distant site, the bird may try to measure the differences $\Delta x = x_p - x_o$ and $\Delta y = y_p - y_o$, where x_p and y_p represent the respective values at the particular site. If the bird is able to determine at least the sign of, for example, Δy, and if he knows the direction of the y gradient (grad y), he may produce a movement tendency that is directed

toward the line y_0. Let us assume, however, that he is unable to recognize the sign of Δx within a broad zone at both sides of the line x_0 (limited by the ,,threshold lines" Tx_1 and Tx_2). Then the bird does not know whether he has to fly the x gradient (grad x) upward or downward. Nevertheless, it may be a useful strategy to produce a movement tendency that is oriented to either of the two directions. If the bird follows both of his tendencies, his actual flight path may lead him in a direction somewhere between those two components. By this way he will approach the zero line or null-axis y_0. However, he will not approach it perpendicularly, but in an acute angle because of the influence of the x component which is oriented more or less along this line. After arrival at his axis the bird will follow it until he either reaches his home or the threshold line Tx_1 at which he realizes that he is on the wrong side and reverses his direction, following now the null-axis ,,backward".

For possible modifications and complications of this scheme see WALLRAFF (1974). In its simple form, the scheme has been applied to the Würzburg results as they exist so far. The black arrows in Fig. 2 represent real data, while all other lines are theoretical. They are optimally adapted to the results in the following ways: (1) grad x, polarized toward NNW, is the PCD that results as an overall mean of the bearings at the 16 release sites; x_0 is perpendicular to this direction. (2) The ,,null-axis" y_0 is calculated as that line (out of all possible straight lines running through home) toward which the overall mean component of the 16 sites is maximal. Each of the mean vectors (arrows) is split then into two components according to the two gradients. With three exceptions, all components follow the general rule: along the x gradient with polarization to the PCD, and along the y gradient toward y_0. One of the exceptions (60 km south) is connected with a vector length near zero and therefore does not mean very much. The other two agree with the hypothesis: They are at the farthest distances in the north and can be interpreted as being close to or beyond the threshold line Tx_1 at which the birds may realize that they have to reverse the sign of their x component.

If all the many variables are considered that may influence the initial bearings of pigeons, and if it is considered that neither a possible system of coordinates nor the way in which birds make use of it is necessarily so simple as described here, the degree of coincidence between data and hypothesis appears fairly good.

Conclusion

Coming back to the problem of compass orientation and goal orientation, we have to distinguish two points of view: On the one hand, we have to handle the data as neutrally as possible without any specific hypothesis in mind. Then we have to speak of goal orientation in a purely operational sense, i.e., in such cases only in which geometric relations to the goal can be distinguished from other directional preferences. On the other hand, it is rather naive to expect that the birds always should be able to determine the direct airline route towards home and that this route is the most adequate line of reference. Therefore one should do both, at first ascertain whether goal orientation does exist, for which purpose no other reference is available, and as a second step one may ask why the birds decide for those directions which they do actually choose.

The null-axis hypothesis is able to explain the pattern of ,,release-site biases" without claiming physical anomalies either at the home site or at the sites of release. (However, anomalies may contribute to the deviations from a regular pattern.) Further, it is able to

integrate the PCDs into a general system of navigation. It is a consequence of this hypothesis that there is, in a merely descriptive sense, some degree of goal orientation, but also some degree of compass orientation. This should be kept in mind when the effects of certain treatments are investigated. If at one site, or at several sites asymmetrically located with respect to the loft, the treatment does not appear to have an effect an the pigeons' bearings, this need not mean that their homeward orientation is not affected by this kind of experiment: the observable orientation may be based on a still persisting PCD. On the other hand, if an effect of the treatment is obvious, this need not concern the degree of homeward orientation, but might be due to a change (e.g.; a reversal) of only the PCD (cf. Wallraff 1979). These aspects have to be considered when experiments are conducted, and the data have to be evaluated in a way that permits a decision between the different possibilities.

As with many other effects in pigeon homing, it is difficult to estimate the importance of the PCDs within the navigational system. However, we should pay attention to each hint even if we do not see, at the moment, obvious connections to other effects. It is a cardinal weakness of the above concept that nobody knows whether coordinates in the described sense do exist, and if so, what their physical bases might be. On the other hand, home flights of pigeons take place in peculiar patterns which cannot be explained as yet on the basis of the physical cues that are thought to be involved in bird navigation. Thus, both approaches should be followed independently: the analysis of the role of certain environmental cues as well as the analysis of the system of flight movements. Finally, of course, all aspects have to be synthesized, but no speculative attempt of that sort shall be made here.

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CONVENER: V. D. ILJITSCHEW

Oekologische Ansätze zur Klassifikation der Adaptationen des Hörsystems

W. Iljitschew

Experimentelle Methoden erbrachten neues Faktenmaterial, dessen Umfang ständig wächst und darum optimale Strategien für weitere Untersuchungen erforderlich macht.

Das Auffinden von Adaptationen und oekologischen Korrelationen

Die Vielfalt von Adaptationen erschwert ihre Klassifizierung. Ein bedeutender Teil von ihnen ist noch unbekannt. Es ist angebracht, sich auf oekologische Korrelationen zu konzentrieren – Adaptationen, die auffällig mit konkreten oekologischen Faktoren korreliert sind. Sie sind besser zugänglich und oft bereits gut untersucht. Das Auffinden oekologischer Korrelationen basiert auf dem Phänomen der oekologischen Parallelismen (Abb. 1 A). Wenn man eine Reihe aus Vertretern einer systematischen Gruppe aufstellt, die sich durch den Grad ihrer oekologischen Anpassung an ein und denselben Faktor unterscheiden, und dabei die weniger spezialisierten an die Basis und die höher spezialisierten Arten an die Spitze stellt, dann prägt sich das untersuchte Merkmal nach oben hin stärker aus. Stellt man eine analoge Reihe in einer anderen systematischen Gruppe auf, die sich an den gleichen Umweltfaktor angepaßt hat, kann man beobachten, daß sich das untersuchte Merkmal ähnlich – parallel – verändert. In diesem Fall ist es möglich, festzustellen, daß das Merkmal mit dem gegebenen oekologischen Faktor korreliert ist.

Autonomie und Systemcharakter des Entstehens von Adaptationen

Oekologische Korrelationen treten in der Mikro- und Makrostruktur des Ohrgefieders, des Trommelfells, der Extracolumella, des Stapes und der Muskulatur des Mittelohres, der Basiliarmembran und der Rezeptoren der Cochlea, des Hörnervs, der einzelnen Hörneuronen und ihrer Dendriten, der neuronalen Komplexe und der Hörkerne auf. Die autonome Einheit der adaptiven Veränderlichkeit wird durch die einzelnen Abschnitte dargestellt (Außen-, Mittel- und Innenohr, Hörkerne). Als funktioneller Bestandteil des Hörsystems besitzt jeder Abschnitt funktionelle und strukturelle Autonomie. Mit Hilfe seiner strukturellen Möglichkeiten löst er selbständig funktionelle Aufgaben. Mit den oekologischen Faktoren kommen die meisten Abschnitte nur mittelbar über vorgeschaltete Abschnitte in Verbindung, da diese das oekologische Signal nur transformiert weiterleiten. Das Signal enthält jedoch eine direkte Information über die Umwelt. Da die Abschnitte im Hörsystem streng aufeinanderfolgen, besitzen sie eine unterschiedliche Stellung gegenüber der Umwelt (Abb. 1 B). Das Außenohr hat direkten Kontakt mit der Umwelt, das Mittelohr besitzt einen und das Innenohr zwei vorgeschaltete Abschnitte usw. Daher wirken sich die oekologischen Korrelationen an der Peripherie des Hörsystems stärker aus (Prinzip der Lateralisierung). Das zeigt sich ebenfalls in der alternativen Spezialisierung benachbarter Abschnitte. So besitzt das Außenohr von tauchenden Vögeln Anpassungen, die das Trommelfell vor Wasser schützen, aber gleichzeitig den Schall dämpfen. Das Mittelohr hingegen hat schallverstärkende Anpassungen (Abb 1 C).

Severzow-Institut für Evolutionsmorphologie und Oekologie der Tiere an der Akademie der Wissenschaften der UdSSR, Moskau, UdSSR.



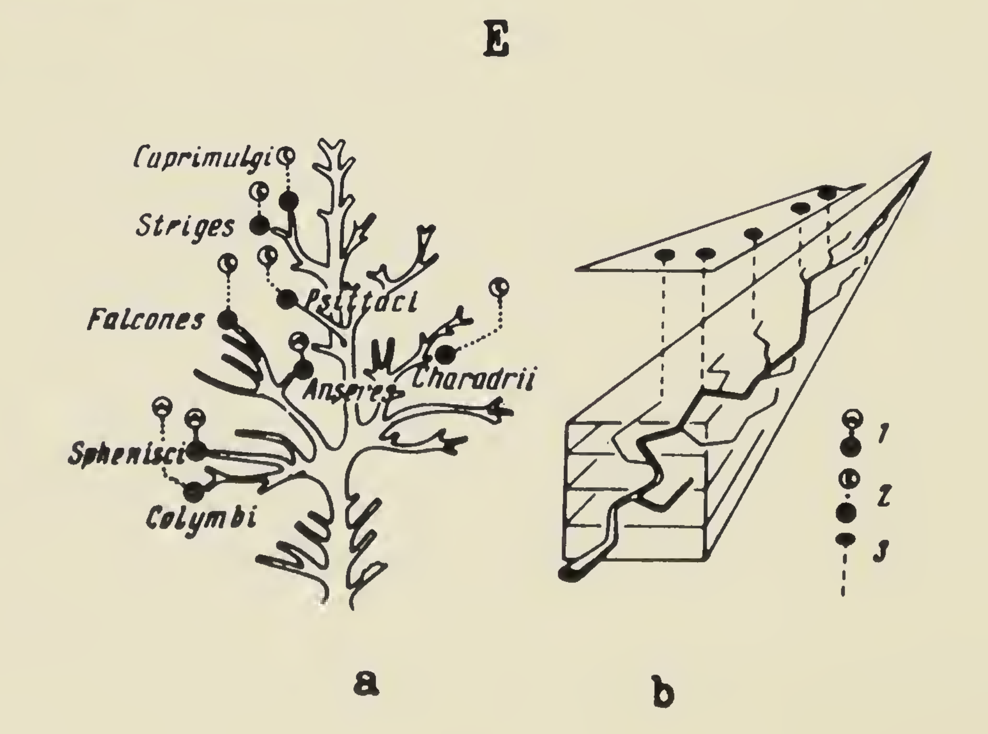
Abb. 1. Grundphänomene der adaptiven Variabilität des Hörsystems.

A – oekologische Parallelismen und Auffinden der Korrelationen (schematisch : aufgefundenes Korrelat – quadratische Form).

B – Autonomie und Systemcharakter des Auftretens oekologischer Korrelationen. 1, 2, 3, 4: Abschnitte des Hörsystems; a: akustisches Signal als Umweltfaktor; B: mit unterbrochenen Linien sind mögliche Korrelationen zwischen einzelnen Abschnitten und Umweltfaktoren angedeutet.

C – Phänomene der Lateralisierung (links) und der alternativen Spezialisierung (rechts), Korrelationen an Beispiel der oekomorphologischen Reihen ortender (links) und tauchender (rechts) Vögel. Die oekologische Spezialisierung der Arten (a, b, c, d) wächst von d zu a hin. 1: Korrelationen, die das Gehör schwächen; 2: Korrelationen, die das Gehör stärken.

E – mosaikartiges Auftreten oekologischer Korrelationen in der Evolution des Hörsystems (a). 1: Korrelationen, die mit dem Wasserleben verbunden sind; 2: Korrelationen, die mit dem Auffinden einer akustisch aktiven Beute verbunden sind; 3: Korrelationen bilden eine Etage höherer Spezialisierung über der Linie der allgemeinen Vervollkommnung des Hörsystems (b).



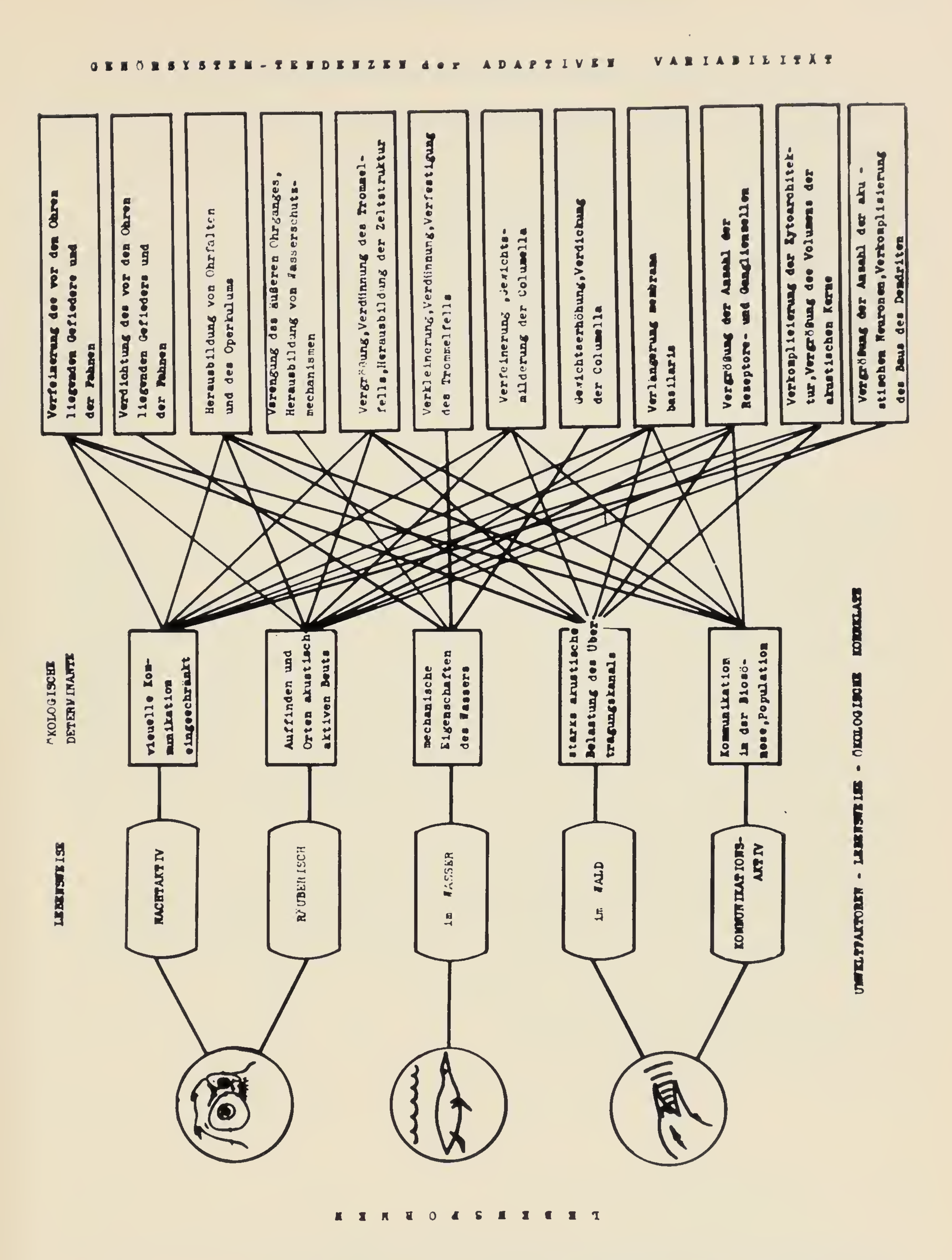


Abb. 2. Zusammenhang der oekologischen Korrelationen mit Lebensweise und Umweltfaktoren.

Mosaikartiges Auftreten von Adaptationen

Die adaptive Veränderlichkeit tritt auf verschiedenen Niveaus des Hörsystems ungleichmäßig auf. In Abhängigkeit von der oekologischen Spezialisierung der Art erstrecken sich die oekologischen Korrelationen über einen oder wenige Abschnitte. Diese Abschnitte führen damit zur oekologischen Spezialisierung des Hörsystems im Ganzen. In der Evolution führt dies zum mosaikartigen Auftreten oekologischer Korrelationen (Abb. 1 E). Ähnliche Korrelate kann man auf höheren und niedrigen Niveaus und in Seitenästen der Evolution finden. Sie treten in manchen Etappen auf, verschwinden in anderen, um später wiederaufzutauchen. Die Natur hat ein beschränktes Reservoir von Möglichkeiten, und falls oekologische Aufgaben es erfordern, bilden sich in verschiedenen Gruppen ähnliche Merkmale heraus. Es werden fertige Standardlösungen angewandt. So entstehen parallele Korrelationen.

Oekologische Parallelismen – Grundlage einer Klassifikation

Eine Klassifikation der Adaptationen steuert die Untersuchungen der adaptiven Variabilität, lenkt sie in eine bestimmte Richtung. Die Klassifikation muß von oekologischen Faktoren ausgehen, da das Auftreten von Adaptationen von der Umwelt determiniert wird. Eine prinzipielle Möglichkeit zur Klassifizierung gibt das Phänomen der oekologischen Parallelismen. Wenn wir oekologische Korrelationen benutzen, engen wir den Kreis der zu klassifizierenden Objekte und damit auch die oekologischen Faktoren ein. Das erleichtert die Aufgabe wesentlich. Wir haben versucht, Korrelationen und mit ihnen gekoppelte oekologische Faktoren in einem einheitlichen Schema darzustellen (Abb. 2). In einigen Fällen sind die Verbindungen einfach (eine Korrelation – ein Faktor), in anderen Fällen kompliziert (eine Korrelation – mehrere Faktoren; mehrere Korrelationen – ein Faktor). Zwischen den oekologischen Faktoren besteht eine Rangordnung, was sich im Auftreten der Korrelationen widerspiegelt.

Die bereits dargelegten Schwierigkeiten bei der Klassifizierung der Adaptationen gestatten bisher nur, ein Arbeitsschema aufzustellen, das weiter ergänzt und verbessert werden muß. Unsere Vorstellungen darüber haben wir veröffentlicht (Iljitschew, 1974).

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Frequency Selectivity in Parakeet Hearing: Behavioral and Physiological Evidence

James C. Saunders

Introduction

The problem of signal resolution in avian hearing is an important one, particularly because of the varied and complex vocalizations produced by many species. The question of whether or not a bird can process all the acoustic information contained in its song is one which has not really been answered and depends in part on an understanding of the frequency resolving power of the avian ear. One way of determing frequency resolution is by studying tuning curves and the present report describes tuning curves in the Parakeet measured at both the behavioral and physiological level of analysis.

Experiment 1: psychophysical tuning curves

Methods

Eight Parakeets *(Melopsittacus undulatus)* served as subjects. They were trained with avoidance conditioning to respond (by biting a metal rod located in front of their beak) whenever they heard a tone stimulus. The procedures of training have been detailed elsewhere (Dooling & Saunders, 1975). When avoidance learning was well established a modified method of limits was introduced (Saunders, 1976) and this was used to measure absolute thresholds in the quiet. After the audibility curve was estimated a pure-tone masking procedure was introduced. Two stimuli were used: a masker, which occurred continuously in the test environment and a probe tone to which the birds had to respond. All testing took place within a sound attenuated room and the sound pressure level (SPL) of the tones were calibrated in dB re 20 $\mu N/m^2$. Nine probe-tone frequencies adjusted to a 10 dB sensation level were employed. The masker tone was set at a very low intensity (-20 dB SPL) and as the bird responded correctly to successive probe trials, the masker SPL was systematically increased. The psychophysical tuning curve (PTC) represented the masker SPL, at various test frequencies, that disrupted the behavioral detection of the probe tone (Saunders et al., 1978c). An additional procedure was introduced in which a narrow-band noise (45 Hz wide) was substituted for the probe tone. Two such narrow bands, centered at 1.6 and 3.5 kHz, were used and this stimulus was also set to a 10 dB sensation level. Tuning curves were obtained for both these probe signals.

Results

Figure 1 illustrates the absolute thresholds measured in the quiet for the Parakeet, as well as the PTCs for nine probe-tone frequencies between .315 and 6.0 kHz. The characteristic tuning of these curves, as indicated by the sharpness of their "V" shape, generally

Co-authors: John J. Rosowski and Robert L. Pallone.

Author's address: Department of Otorhinolaryngology and Human Communication, University of Pennsylvania, Philadelphia, PA., U.S.A.

increased as higher frequency probe tones were examined. The PTCs obtained at 1.6 and 3.5 kHz using the narrow-band probe signals appear in Figure 2. These curves also indicate that the higher frequency PTC (3.5 kHz) is more sharply tuned than the lower frequency tuning curve. The masking function for both these PTCs was examined in the low frequencies and both show the long tail characteristic of mammalian tuning curves. Interestingly, the trough of the tuning curves in Figures 1 and 2 seem to be: a) somewhat deeper than that seen in mammalian tuning curves, and b) symmetrical in their rate of roll-off on the high and low frequency side.

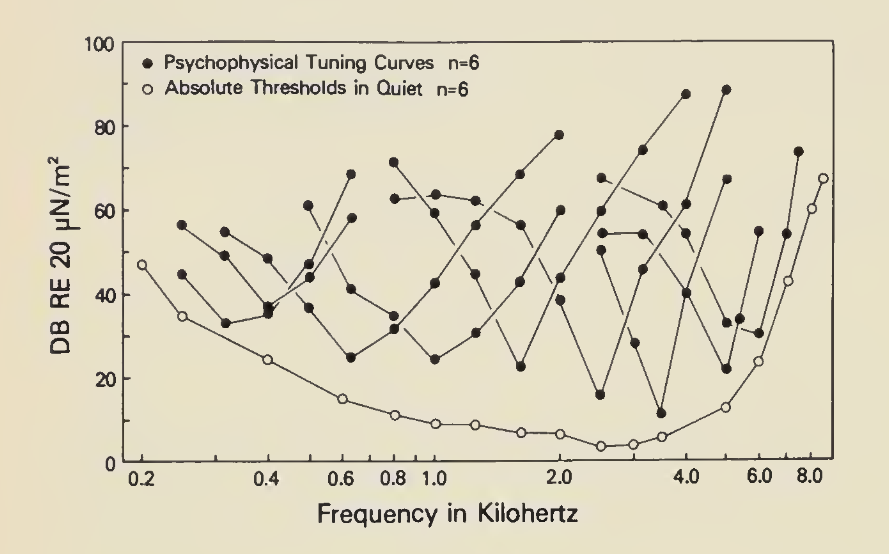


FIGURE 1. Nine PTC plotted as dB relative to SPL. The absolute threshold in the quiet is also known. The largest standard error over all the PTC masker frequencies was ± 6 dB.

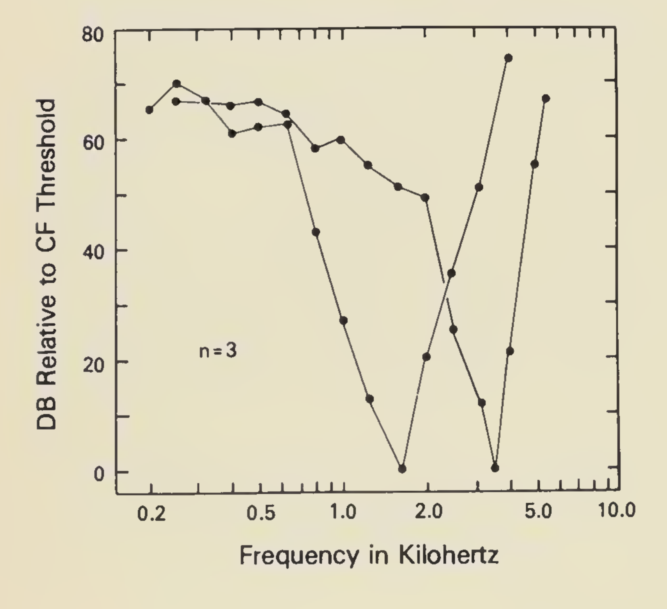


FIGURE 2. Two PTC using a narrow-band noise probe signal. Both curves have been normalized by plotting the masked thresholds as dB relative to the CF threshold.

Experiment 2: evoked response tuning curves

Methods

Five adult Parakeets served as subjects. Each was anesthetized with Urethane (.05 cc of a 20% solution) and was mounted in a specially designed head holder. The cerebellum was exposed and a bipolar electrode was lowered into the region of the cochlear nuclei (CN).

A simultaneous masking procedure similar to that used in Experiment 1 was employed in this study. However, the dependent variable was the masker SPL required to abolish the probe-tone evoked response. The probe tone consisted of a 40 msec tone burst (5 msec rise/decay time) presented at a rate of 10 per second. The evoked activity at the electrode

was amplified and signal averaged over 128 samples. After the electrode was placed in the CN the evoked response visual detection level (VDL) threshold was determined at each of six probe-tone frequencies. The probe tone was then set to a level 15 dB above the threshold and continuous masking tones were introduced at various frequencies. The SPL of the masker that eliminated the probe tone evoked response was noted. This procedure is similar in part to that described by CHEATHAM & DALLOS (1975).

Results

The masking curves for six probe-tone frequencies averaged over the five animals appear in Figure 3. The data in these tuning curves have been normalized by setting the center frequency (CF) to zero dB and plotting all other masked thresholds relative to this point. The sharpness of the curves clearly increased as higher frequency probe tones were tested. Moreover, within 30 to 40 dB of the CF the high and low frequency slopes of the tuning curves appear very symmetrical.

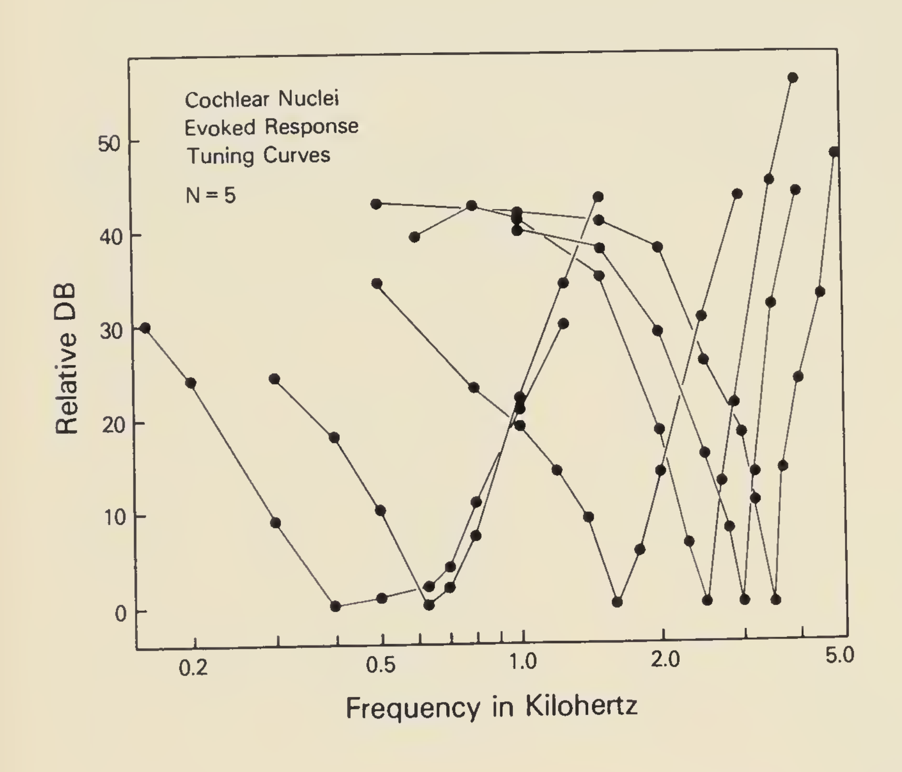


FIGURE 3. Cochlear nuclei evoked response tuning curves averaged in 5 birds for 5 probe tone frequencies. The curves are normalized and plotted as dB relative to the CF threshold.

One way of assessing the frequency selectivity of tuning curves is to calculate a "Q" ratio (SAUNDERS et al., 1978c). Briefly, "Q" represents the ratio of the CF of a tuning curve and the bandwidth of the curve 10 dB above the CF. When the value of "Q" is small it denotes broad tuning; when "Q" is large it indicates sharp tuning. Since "Q" is a ratio, the relative frequency selectivity of tuning curves with varying CFs can be directly compared within a subject, among subjects, and even between experiments if the 10 dB point is used to calculate bandwidth.

The "Q" values for the tuning curves in Figures 1, 2 and 3 are presented in Figure 4. The "Q" of the critical band is also included (SAUNDERS et al., 1978b). As can be seen frequency selectivity is poor (broadly tuned) from 0.4 to 1.6 kHz, becomes better (more sharply tuned) above 2.5 kHz, reaches a peak at 3.5 kHz, and then deteriorates rapidly (again becomes more broadly tuned) above 4.0 kHz.

Discussion

In the first experiment narrow bands of noise were substituted for pure tones as the probe signal. The narrow bands of noise have proven effective in other studies in eliminating the occurrence of acoustic beats when probe tone and masker have nearly identical frequencies (SAUNDERS et al., 1978a). The present results, however, indicate that the shape of the tuning curves were nearly identical with both procedures and this suggests that the occurrence of acoustic beats may be less of a problem in masking experiments with birds than with mammals (SAUNDERS & ELSE, 1976; SAUNDERS, 1976; SAUNDERS et al., 1978c). The nine PTCs in Figure 1 were obtained at a probe-tone sensation level of 10 dB. The average threshold shift at the CF over all nine PTCs was 9.5 dB. Thus, at the CF, the probe tone was most effectively masked by a second tone of similar frequency and intensity. In all of the tuning curves illustrated in Figures 1 and 2 the rate of high and low frequency roll-off was nearly identical. This sort of observation is frequently made for low frequency tuning curves in mammals; however, at high frequencies mammalian tuning curves become asymmetrical, with the high frequency portion of the trough showing a greater roll-off rate than the low frequency portion (SAUNDERS et al., 1978d).

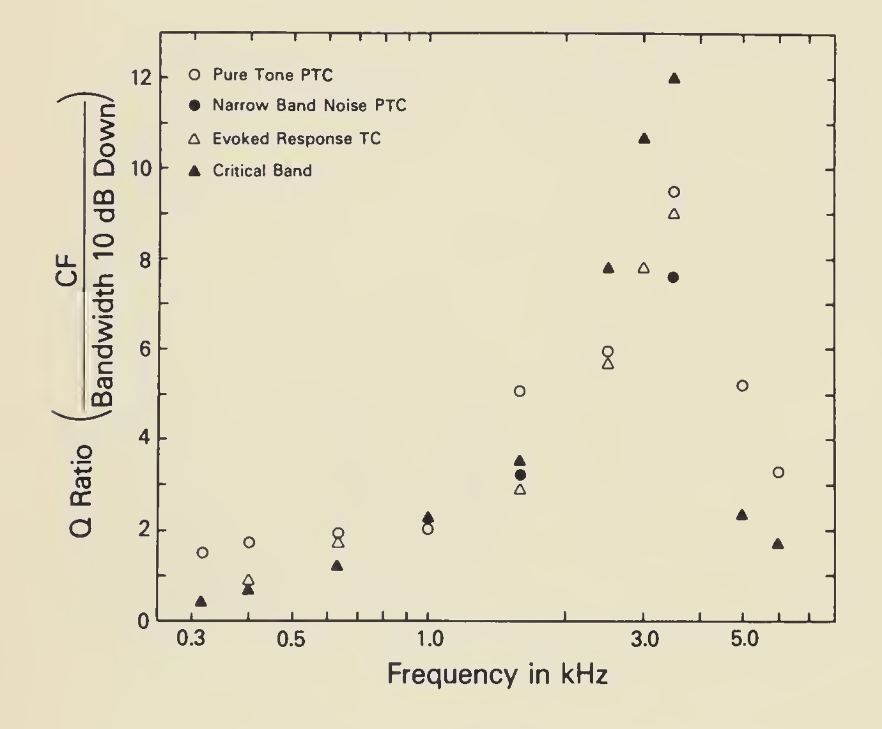


FIGURE 4. The Q ratio from various tuning curves and the critical band is plotted as a function of the CF. The parameter of the figure is data from four experiments. It is interesting that the shape of the "Q" CB curve is nearly identical to that observed with the "Q" of the tuning curves. This suggests that the critical band is determined by the same frequency selective mechanisms that shape the tuning curves. It is purely coincidental, however, that the "Q" values of to CB are similar to the "Q_{10dB}" values of the tuning curves.

The shape of the evoked response tuning curves is remarkably similar to that of the PTC of Figure 1 and 2. Indeed, the values of "Q" as shown in Figure 4 are virtually the same. While these data need to be expanded further, particularly the evoked response tuning curves into the high frequencies, they offer some intriguing possibilities. Correlations between evoked response and psychophysical tuning curves may be more valuable than those between single fiber and behavioral tuning curves, because the former pair both represent the activity of populations of neurons. Indeed, the present data are so strikingly similar as to suggest that the frequency selectivity observed in the PTC originates within or more peripheral to the CN.

Finally, the results of four experiments when plotted as relative frequency selectivity ("Q") exhibit remarkable similarity (Figure 4). Frequency selectivity in the Parakeet is best

between 2.0 and 4.0 kHz. This frequency region also contains the most sensitive thresholds measured in the quiet, the smallest frequency difference thresholds, smallest critical ratios, and is the region of dominant frequency energy in Parakeet vocalizations (DOOLING & SAUNDERS, 1975).

Acknowledgements

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Morphology of the Bony Stapes (Columella) in Birds: Evolutionary Implications

ALAN FEDUCCIA

Introduction

Because of the morphological uniformity of birds their phylogenetic relationships are poorly known. And despite more than a century of comparative morphological studies there are few characters that have enabled students of avian evolution to relate the various orders. Therefore discoveries of new characters for which primitive-derived sequences can be demonstrated (HENNIG, 1966; CRACRAFT, 1972) may be of great important in resolving avian relationships.

The stapes is one of the last remaining elements of the avian skeleton to be examined, no doubt because of its minute size (one to several mm) and its remote location in the recesses of the middle ear. In addition, it is often lost in skeletal preparations. Nearly all cladistic studies of birds have suffered from one major drawback: the inability to establish unequivocally the primitive nature of the character or characters involved. The stapes provides an exceptional and perhaps unique opportunity for phylogenetic analysis in that: (1) the primitive condition occurs in most birds; (2) the primitive nature of the element can be established beyond reasonable doubt as that found in the reptilian ancestors of birds. The primitive condition of the stapes is a simple structure, consisting of a flat footplate that fits into the oval window of the inner ear; its straight bony shaft connects via an extracolumellar and its ligaments to the tympanic membrane.

Two assumptions are made in this analysis. I assume that the primitive condition of the avian stapes, which is found in the vast majority of birds, is homologous with the same element in reptiles, and represents a retained primitive condition. Second, I assume that structurally similar, derived morphologies of the stapes indicate evolutionary relationships, unless there are compelling reasons to assume convergence.

Occurrence of the primitive condition

Only the primitive condition occurs in the vast majority of birds. Slightly derived morphologies of the stapes occur in certain Procellariiformes, Pelecaniformes, Ciconiiformes, and Falconiformes. All of the ratites, the gaviiforms, and podicipediforms, most ciconiiforms (except storks), all anseriforms, most falconiforms (except some eagles), all galliforms, all gruiforms, all charadriiforms, all columbiforms, all psittaciforms, and all musophagiforms possess the primitive condition. Slightly derived morphologies are found in certain groups but carry no phylogenetic information and will not be discussed here. This paper focuses on the morphology of the bony stapes in only these groups in which it is of importance in resolving phylogenetic relationships.

Ciconiiformes and Pelecaniformes

The Ciconiiformes has been considered by many to represent a heterogeneous

Department of Zoology, University of North Carolina, Chapel Hill, N. C., USA.

assemblage, with the ibises and herons not showing any close resemblance to other members of the group. The herons (Ardeidae, including the boatbill, *Cochlearius),* the ibises (Threskiornithidae) and *Scopus* (Scopidae) exhibit the primitive condition of the stapes; the element is therefore of little use in understanding the phylogenetic relationships of these groups. However, all of the storks and the shoebill or whalebill (*Balaeniceps)* have a similar derived stapedial morphology (Feduccia, 1977b). The stork stapes is characterized as a broadly tubular structure that enlarges slightly at the footplate region, and exhibits numerous fenestrae along the entire surface, often with one or several larger openings at the base near the footplate. The similarity of the stapes in storks and the whalebill argues strongly that the storks as presently defined are monophyletic and that *Balaeniceps* fits in with the group. Pelecaniform birds have a variety of stapedial morphologies (Feduccia, in prep); however, two basic types may be distinguished. The primitive pelecaniforms (*Phaethon)* share a similar stapedial morphology with the storks, but most pelecaniforms have a morphology that is more highly derived, producing a very elongate tubular structure that is often curved along its length. Thus, a pelecaniform-stork relationship cannot be negated by the stapedial evidence.

Strigiformes

The owls are placed typically in a single order that is divided into two distinctive families, the true owls (Strigidae) and the barn owls (Tytonidae). Further subdivisions split the Strigidae into two sub-families, the Buboninae and Striginae; the Tytonidae into the Tytoninae and Pholininae. The last taxon has been the source of much controversy for many years, with some authors placing the bay owls (*Phodilus)* with the strigids rather than the tytonids. *Phodilus* and *Tyto* have a nearly identical derived morphology of the stapes (Feduccia, 1978). A somewhat similar derived condition is found within *Strix.* The derived stapes of *Phodilus* and *Tyto* differs from that in *Strix* not only in the degree to which the footplate protrudes into the oval window, but also in the means of its attachment to the shaft. In *Tyto* and *Phodilus* the shaft broadens at the base to meet the footplate at its periphery, making the shape similar to that of an inverted ice cream cone. In contrast, the shaft of *Strix* attaches nearer the center of the footplate, causing the stapes to appear umbrella-shaped. In addition, the three species of *Strix* examined *(nebulosa, occidentalis,* and *varia)* vary considerably in the degree of protrusion of the footplate into the oval window, from almost none in *S. nebulosa* to a very marked protrusion in *S. varia.* Thus, the modified morphology of the stapes in *Strix* appears to have evolved independently of that of *Tyto* particularly since none of the other genera of Strigidae possess such a derived character.

Coraciiformes

The order Coraciiformes as delimited by Wetmore (1960) is one of the most heterogeneous of the avian orders, yet most classifications since the time of Linnaeus (1758–59) have agreed upon the general relationship of the families which he included within the order. On the other hand, the naturalness of the order may be open to considerable question. Are the families included within the order actually related, or do they represent a variety of passerine related families of primitive stocks, or moderately diverse and bizarre forms? As W. Sclater (1924) noted, "...The Coraciiformes have for

many years been loaded with a heterogeneous collection of forms which custom has blindly accepted." LOWE's (1946) analysis of *Upupa* which indicated that in some characters it was typically coraciiform, in others typically passerine or picine, probably summarizes the characters of coraciiform birds in general.

Upupidae and Phoeniculidae

Although the relationships of all the coraciiform families is still a completely open question, one intriguing question concerns the supposed affinity of the hoopoes (Upupidae) and the wood-hoopoes (Phoeniculidae). The complex and interesting history of the vicissitudes of the classification of these birds is completely covered in SIBLEY & AHLQUIST (1972). LINNAEUS (op. cit.) placed all of the coraciiform families (sensu WETMORE, op. cit.) in an order Picae, and *Upupa* was placed next to *Certhia*. Since that time there have been suggestions of relationship of the hoopoes to coraciiform families, especially the hornbills (Bucerotidae), and also to the sunbirds, starlings, crows, and the birds-of-paradise. The possible relationship of the hoopoes to the wood-hoopoes has also been open to considerable question. SIBLEY and AHLQUIST (op. cit.: 230) concluded from their egg white protein data that, "...we cannot support or deny a close relationship between *Upupa* and the Phoeniculidae." Both families are characterized by the common possession of a derived morphology of the bony stapes which is found in no other avian species (FEDUCCIA, 1975a). This type of stapes is characterized by a flat bony footplate, but with a short but wide shaft that bifurcates into two processes. There is a long, laterally directed thin process, and a shorter, broad process, both of which connect to the tympanic membrane via extracolumellar ligaments, and no doubt function in a complex lever system.

The possession of this bizarre type of stapes in both the Upupidae and Phoeniculidae is interpreted as a strong indication of monophyly of the two families.

Trogonidae, Alcedinidae, Todidae, Meropidae, and Momotidae

All of the species of trogons examined exhibit a derived morphology of the stapes indistinguishable from the same element in the coraciiform families Alcedinidae, Todidae, Meropidae, and Momotidae (FEDUCCIA, 1975b, 1977a). The bee-eater, kingfisher, motmot and tody assemblage would thus appear to represent a monophyletic assemblage and trogons are no doubt derived from the group; for convenience they may all be placed in a separate order, the Alcediniformes.

The stapes differs in only one major respect from the type found in "suboscine" passerine birds (see suboscine section). This stapes differs from the primitive condition in having a large, hollow, bulbous basal and footplate area that exhibits a large fenestra only on one side. Sometimes the fenestra is subdivided. The fenestra leads to a large hollow fossa. Because of this morphology of the basal and footplate areas, the stapedial shaft is shifted in position from the middle of the base to the periphery, thus seemingly producing a different type of lever system. Variation between the Trogonidae, Alcedinidae, Todidae, Meropidae, and Momotidae ("alcediniform birds") is minor. The Alcedinidae have the most expanded basal area, and are generally distinguishable from other families by that character.

The families under consideration may also be characterized by the position of the shaft of the stapes with respect to the base. This character is best described by imagining the

form of the base of the stapes as a protractor with a slightly rounded base, from the middle of which the shaft emerges.

Other coraciiform birds and possible allies

The swifts and hummingbirds (Apodiformes), colies (Coliiformes), cuckoo-rollers (Leptosomatidae), ground-rollers (Brachypteraciidae), true rollers (Coraciidae), and most hornbills (Bucerotidae) all exhibit the primitive condition of the stapes. In addition, most of the piciforms also have the primitive condition.

Passerine birds

Suboscine species examined have a derived stapes only slightly different from that of the Trogonidae, Alcedinidae, Todidae, Meropidae, and Momotidae. The number of specimens of suboscine birds examined is given in Feduccia (1974). In the oscine passerine birds the primitive condition is found in all families. There is minor variation in the basal region, but it is fundamentally similar in all forms. As in the trogons, kingfishes, todies, bee-eaters and motmots, the suboscine stapes has a large, hollow, bulbous basal and footplate area that exhibits a large fenestra on one side only (sometimes the fenestra is subdivided) which leads into a large fossa. As in the coraciiform groups, the shaft attaches to the periphery of the base. The "suboscine" stapes differs from the alcediniform stapes in the shape of the base and the position of the shaft. In suboscines, the footplate is nearly triangular, with three unequal sides, but with the shaft usually emerging from the area where the two longest sides meet. The shape of the footplate, and the point of emergence of the shaft of the stapes is highly variable in suboscines, while in the alcediniforms it is a static character. By this character alone one can separate suboscines from the alcediniform groups with a confidence of over 90%; however, in some suboscines the base resembles the alcediniform type. This difference in the form of the base of the stapes may also be demonstrated by placing specimens in a finger bowl or depression slide filled with a 50% glycerine solution. Alcediniform stapes will turn so that the fossa faces upward, while "suboscine" stapes will tend to fall on their "sides."

Suboscines with the derived stapedial morphology may be separated from other passerines as an order Tyranniformes; they would appear to form a cohesive monophyletic group.

Australian "Suboscines"

Evidence has accumulated to indicate that the Menurae is not of suboscine, but probably of oscine affinity (Sibley, 1974; Feduccia, 1975c). I have now examined the stapes of *Menura, Atrichornis, Acanthisitta,* and *Xenicus;* all lack the stapedial morphology characteristic of modern suboscines and have the primitive condition for the element. Though possession of the primitive condition of the stapes in these forms does not prove their oscine affinities, it suggests that they are not close allies of the modern suboscines, or at least would have had to evolve before the derived stapes type. Therefore it seems more likely that the species of Australian passerines thought previously to represent suboscines are probably oscines or are primitive within the passerines. The suboscines of Madagascar have the suboscine type of stapes, thus confirming their status within the Tyranni (Feduccia, 1975d).

Conclusion

The morphology of the bony stapes provides an exceptional and perhaps unique opportunity for phylogenetic analysis in that: (1) the primitive condition is known, it being that found in the reptilian ancestors of birds; and (2) the primitive condition (with a flat footplate and straight shaft) occurs in the vast majority of living birds. The primitive condition is assumed to represent the retained reptilian stapes, and therefore where derived "pockets" of unique stapedial morphologies are found they are interpreted as strong indications of evolutionary relationships.

Derived morphologies occur only in a number of cases, but a cladistic approach to stapedial morphology permits a number of probable evolutionary statements as follows: (1) the storks (Ciconiidae) are a monophyletic assemblage and share a stapedial morphology with the whalebill *(Balaeniceps:* Balaenicipitidae). The primitive pelecaniforms *(Phaethon)* share a similar morphology with many storks (most other pelecaniforms have a more highly derived morphology), so a pelecaniform-stork relationship cannot be negated. (2) Within the Strigiformes, *Tyto* and *Phodilus* share a similar derived stapedial morphology. (3) The bee-eaters (Meropidae), kingfishers (Alcedinidae), motmots (Momotidae), and todies (Todidae) are monophyletic, and the trogons (Trogonidae) are derived from the above assemblage; they may be named the Alcediniformes. (4) The hoopoes (Upupidae) and wood-hoopoes (Phoeniculidae) are monophyletic. (5) The New and Old World suboscines, including the Philepittidae, form a monophyletic assemblage, but are not allied with the Australian forms thought to be suboscines *(Menura, Acanthisitta,* etc.), which forms are shown to be oscines. Suboscines are placed in the Tyranniformes.

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The Relationship between the Microanatomical Development of Auricular/Conch Feathers (limbus facialis) of Owls and their Foraging Ecology

Richard J. Clark, Dana J. Myers, Barry L. Stanley and Leon H. Kelso

Introduction

The development of hearing and its associated anatomy reaches its epitomy in owls, as an order, among birds. It has been researched anatomically and physiologically for only a relatively few species but there has been great depth in those studies. Literature dealing with descriptive anatomy of Strigiformes is exhaustively covered in Norberg (1977) hence there is no need to review it here. It should be noted, however, that Kelso (1940) first pointed out the plastic nature of the external ear, responding, as it were, to climate. Ilyichev (1961) examined the microstructure of feathers of the *limbus facialis* (facial disc) and suggested ecological selection factors impinging upon the evolution of these feathers. Clark & Stanley (1976) examined the microstructure of both facial disc feathers (auricular) and feathers of the postauricular fold (conch) and independently reached conclusions, concerning ecological pressures, that were essentially the same as those of Ilyichev (1961). Dementiev & Ilyichev (1963) examined the ears and associated structures and feather specializations of the ecologically similar Falconiformes. The nature and role of hearing in owls has been physiologically explored by Schwartzkopff (1955, 1962, 1963), Payne & Drury (1958), Norberg (1968, 1973), Golubeva, Chernyi & Ilyichev (1970) Van Dijk (1973), Konishi & Kenuk (1975) and Nieboer & Paardt (1977). Additionally, behavioral experiments have been conducted to ascertain the physiological limitations on hearing in owls (Payne, 1962; Ilyichev & Chernyi, 1973; and Konishi, 1973a,b). Ilyichev (1975) has brought together the literature on research dealing with direct and indirect experimentation as well as those utilizing electro-physiological and histological techniques.

Comprehensive approaches to the problem, from the standpoint of species examined, have been lacking with the notable exceptions of Ford (1967) and Norberg (1977). Also few studies have dwelt on the ecological aspects of hearing with those mentioned earlier, i.e. Kelso (1940), Ilyichev (1961, and others), Norberg (1968, 1970, 1973) and Clark & Stanley (1976) being exceptions.

Ilyichev (1975) has been studying the microstructure of feathers and the internal neuro-anatomy and physiology of owls as have been Knudsen & Konishi (1978). Finally, Norberg (1977) has been systematically researching the descriptive and comparative morphology of the external ears of owls. Both have been interested in the evolutionary aspects of the system. Norberg (1977) pointed out the need to understand the ecological aspects of the problem:

> "To be able to judge the degree of adaptivity of various ear structures and asymmetries one needs to know (i) their function and (ii) their importance in owl ecology. Knowledge of relations between ear structure and function and the species' habitat

First author's address: Department of Biology, York College of Pennsylvania, York, Pennsylvania, USA.

selection and hunting technique is crucial also for the problem of ecological segregation among owls, many species of which are 'searchers'... with wide diets".

To point out the sometimes dynamic balance between the ears, hearing ability, foraging behavior, feeding ecology and habitat of an owl we will use the Short-eared Owl as an example. PYCRAFT (1898) had noted the extensive asymmetry in the fleshy parts of the ear and KURODA (1967) had suggested osteological asymmetry also in this species. It is often stated that this species is diurnal and LACK (1966) had concluded they "hunt by night". Yet PITELKA et al. (1955) noted they must have hunted "in the hours of low light" at Point Barrow, Alaska. CLARK (1975) demonstrated that given a choice, i.e. with an abundant food supply and in the absence of harrassment they are crepuscular. The ecological selection pressure causing them to maintain the anatomical specializations for using acoustical cues to locate prey lies in their propensity for open habitats and in the prey that those open habitats frequently yield. Members of the genus *Microtus* frequently overwhelm all other prey species in the diet of this myophagic owl. Pursuing this further, *Microtus pennsylvanicus* is often the species in North America. This species is a semi-fossorial one that travels in tunnel/runways formed in part by grooves on the ground surface that are enclosed on top by vegetation placed there for that reason by the voles. Thus the owl is "in the dark" when taking this prey. We admit ignorance as to whether this habit is unique to this North American species of *Microtus* or if others of this genus have similar habits in other parts of the world.

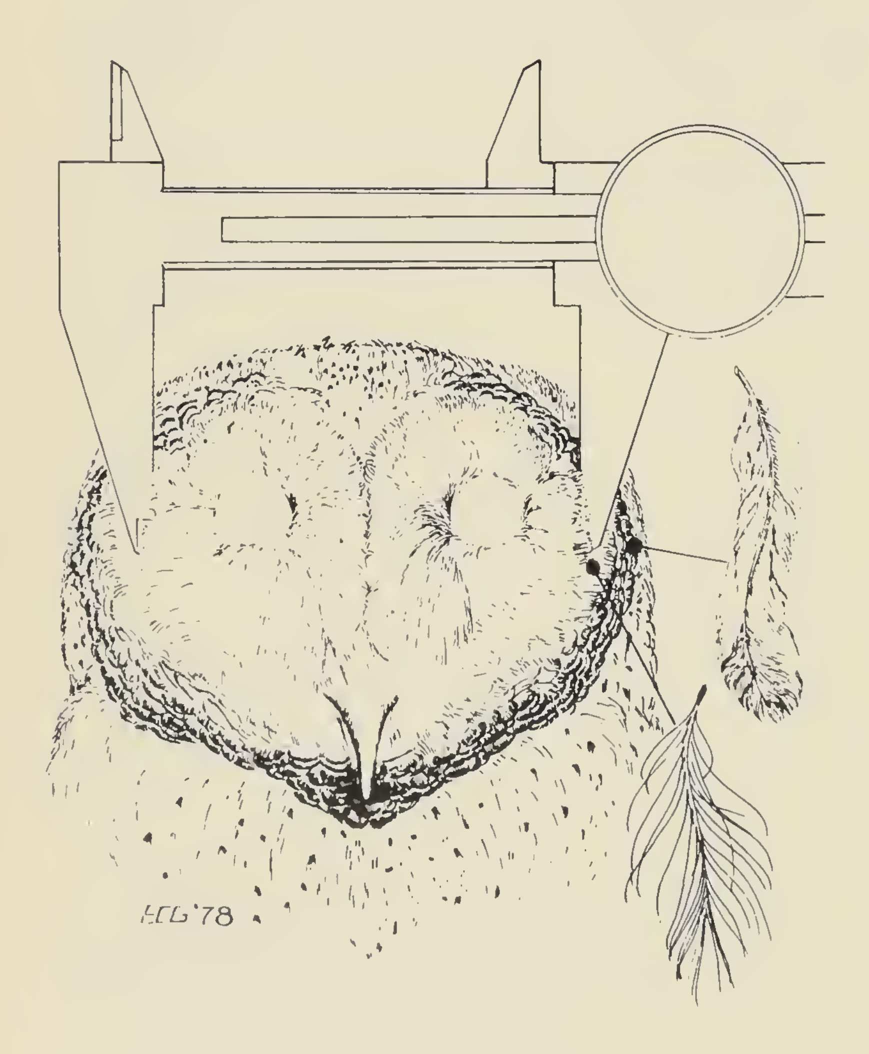


FIGURE 1. Measuring the interaural distance via a dial micrometer. A conch (upper right) and auricular (lower right) feather are also shown.

Methods and materials

All measurements were made from study skins (Fig. 1) housed in the U. S. National Museum (U.S.N.M., Washington, D. C.) and the American Museum of Natural History (New York). Fine measurements were made visually using an optical micrometer. Behavior and food data were drawn from the literature.

Results

Our intent was to do a global survey and this is preliminary to that. We can here only hope to introduce the lines of research that we are pursuing. If the binaural affect (ILYICHEV 1975) serves to facilitate acoustical orientation to a prey source then enlargement of this distance should enhance the owls ability to quickly and accurately ascertain the direction of a sound source. The selection for a wider head would, of course, have to be in balance with all other pertinent selection pressures. It was with these factors in mind that we examined the allometric relationship between interaural distance and body size (Fig. 2).

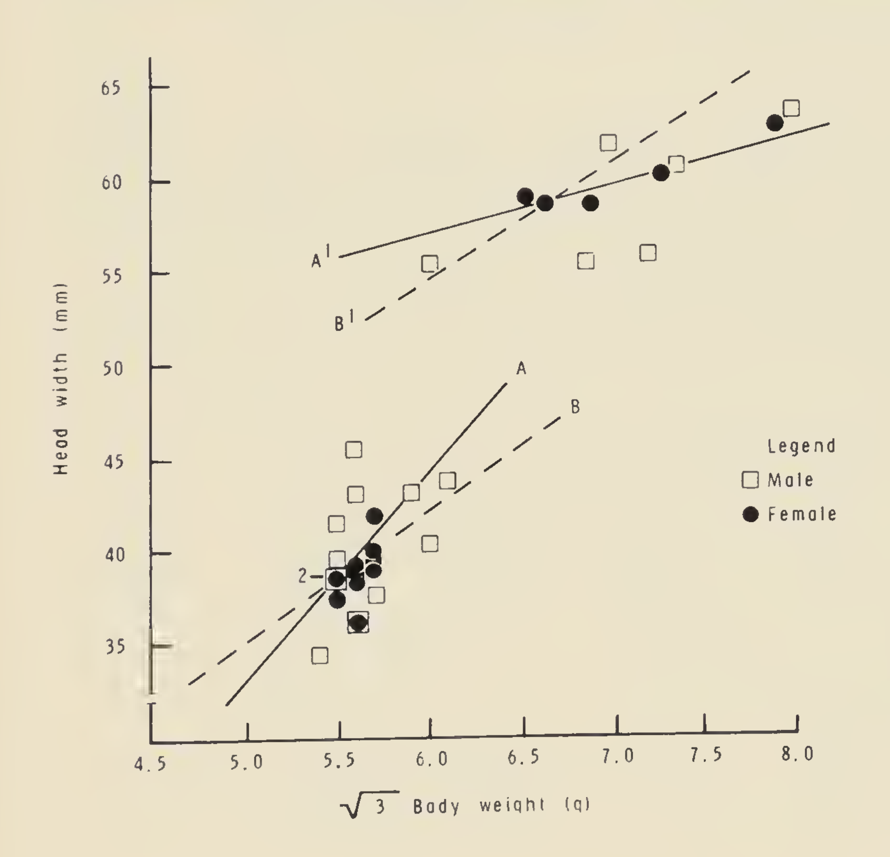


FIGURE 2. Interaural distance regressed against $^3\sqrt{}$ of body mass. *Athene noctua* females (A) and males (B) are below while *Tyto alba* females (A[1]) and males (B[1]) are above. See text for line formulae and statistics. Two equal values are denoted by 2.

Statistics for *Athene noctua* are as follows: (A) ♂ r (correlation coefficient) = .5148, Sig. 0.04, N=12, regression line formula is Y = -24.24879 + 11.32573X, (B) ♀ r = .58419, Sig. 0.04, N = 10, y = -4.10207 + 7.7526X; and for *Tyto alba* (A[1]) ♂ r = .92585, Sig. 0.01, N=5, y = 39.42365 + 2.91073X and (B[1]) ♀ r = .59123, Sig. 0.06, N=8, y = 19.52885 + 5.86629X. We examined several other species which yielded erratic results which we attribute to the crushing of the skulls when the study skins were prepared. The data for the two species presented came from birds collected largely by Dr. GEORGE E. WATSON and presumably prepared under his direction. The *Athene noctua* regression lines are interesting in that they indicate a relatively greater enlargement of the interaural distance for it than for *Tyto alba* with the smallest males showing the greatest enlargement. It should prove interesting to compare these data with some from diurnal raptors.

Ilyichev (1961) examined the microstructure of auricular feathers in several species of owls and Dementiev & Ilyichev (1963) extended this to hawks and also examined facial pterylography. We attempted to push examination of the auricular feathers further (Table 1) but found this examination to have some shortcomings. We extrapolated the physical density of the feathers (AOI) from the measured diameter of the barbs and the number of

Table 1: Towards an acoustical opaqueness index (AOI) for strigiform auricular feathers.

Species	*Tyto alba*		*Otus scops*		*Bubo virginianus*		*Strix nebulosa*		*Asio flammeus*	
	A	C	A	C	A	C	A	C	A	C
Character										
Barbs per mm.	3	4.25	3.25	4.75	3	3	4	3	4	6
Distal barbules per mm.	20.5	37.5	26.5	48	24	29	23	44	38	50
Proximal barbules per mm.	16	35	20.5	38	17	22	17	30	26	36
AOI (%)	12	42.5	21.5	47.5	22	31.5	18.5	40.5	25	48

barbs per mm. We will probably go to measuring density values via a densitometer. It should be noted that pterylography must be considered as is evident in *Strix nebulosa* where the auriculars are set in widely spaced tracts and selection for hearing is probably compromised with selection for reducing heat loss in a cold climate.

It is not surprising that we find flexibility in habitat and diel activity period affinities in owls (Table 2) for food procurement must at times override other preferences. The

Table 2: Habitat and diel activity period affinities for some owls.

Species	*Tyto alba*	*Otus scops*	*Bubo virginianus*	*Athene noctua*	*Strix nebulosa*	*Asio flammeus*
Habitat						
Forest		O	P		P	
Woodland	P	P	O	O		
Savanna	O	O				
Steppe	O	O		P		P
Desert			S	S		
Diel period						
Nocturnal	P	P	P		P?	S
Crepuscular				P?	P?	P
Diurnal	S		S	P	S	S

Preferred = P Occurs = O Sometimes = S

relationship between these factors can be seen rather clearly in *Asio flammeus* (Clark, 1975) where the propensity for frequenting open habitats has lead to stenophagy, flexible fecundity and nomadism in this species. Although the habitat affinity for *Strix nebulosa* is decidedly different than for *Asio flammeus* it too seems to be a plastic species regarding fecundity and hunting times (Höglund & Lansgren, 1968). Both species are myophagic

TABLE 3: Foraging behavior of some owls as reflected by their prey.

Species	*Tyto alba*	*Otus scops*	*Bubo virginianus*	*Athene noctua*	*Strix nebulosa*	*Asio flammeus*
Prey taxa						
Invertebrates	2,059 (0.71)	37 (84.09)	203 (2.12)	600 (10.63)		177 (0.72)
Fish			28 (0.29)			
Amphibians	2,164 (0.75)	1 (2.27)	76 (0.79)	182 (3.22)	21 (0.17)	9 (0.04)
Reptiles	9 (0.003)	2 (4.55)	75 (0.78)	3 (0.05)		2 (0.01)
Birds	6,928 (2.40)		766 (7.80)	157 (2.78)	65 (0.52)	955 (3.86)
Mammals	277,294 (96.13)	4 (9.09)	8,430 (88.01)	4703 (83.31)	12,488 (99.32)	23,572 (95.38)
Total prey number	288,454	44	9,578	5,645	12,574	24,715
Percent	99.99	100.00	99.79	99.99	99.99	100.01

(Table 3) and can take prey using only acoustical cues to locate it. PAYNE (1962) showed that *Tyto alba* also can locate prey acoustically and does so hunting almost exclusively at night. It frequents habitats of a greater variety than the two earlier mentioned species and this is reflected in its diet. The role of hearing versus vison in locating prey, remains to be demonstrated in the other three species for which we tabulated (Table 3) type of prey most frequently taken. Of the remaining three *Otus, Athene* and *Bubo,* the latter is less limited by its size in the prey it can take, and in addition it shows greater plasticity in the habitat it will frequent. There seems to be a decided paucity of data for prey taken by *Otus scops* with some of the tabled data coming from museum skin labels in the U.S.N.M.

One can see that there are large voids of knowledge for even the widely distributed species such as *Otus scops.* There is, no doubt, literature we have not located nor have access to, but we have tried to demonstrate the comprehensive approach required in order to ascertain the importance of hearing for prey location in owls.

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Middle Ear Anatomy of the Struthioniformes

Edward Saiff

Introduction

The relationship of the ratites to each other and to other birds is a controversial topic. Stresemann (1959) suggested that a final solution to this problem may never be reached yet looked forward to further research on the topic particularly in the field of bird anatomy. Bock (1963) noted that while new morphological characters will provide further information it is doubtful whether additional knowledge of morphology can resolve the problem.

What follows is not an attempt to solve once and for all the ratite problem but simply an analysis of middle ear structure of one group of ratites, the Struthioniformes. It is hoped that such an analysis will shed some additional light on this perplexing and interesting problem.

The work is grounded on the notion as in similar previous studies (Saiff, 1974, 1976, 1978) that the morphology of the middle ear region could be trusted as an indicator of taxonomic relationship. Whether or not this study will result in a better understanding of the ratite problem will not be known until similar analyses are made of other ratites and comparisons are made among ratites and carinates.

Anatomy of the middle ear region

The middle ear is a large concavity taking up much of the posterolateral region of both sides of the head. The tissue comprising the middle ear sac is supported anteriorly and dorsally by the quadrate, posteriorly by the extensive paroccipital and metotic processes and ventrally by a thin process in the rear (and, more anteriorly, the lateral edge) of the basitemporal platform. The interior wall of the middle ear cavity is an extensive excavation bounded dorsally by a shallow depression of the skull filled by musculature, the upper tympanic recess, behind which is located the articular surface of the paroccipital process for the otic head of the quadrate. No portion of the upper tympanic recess extends posterior to the quadrate-paroccipital articulation.

The middle ear cavity is referred to as the tympanic fossa since it is covered by the tympanic membrane and contains the columella. The inner wall of the tympanic fossa is made up by the periotic and exoccipital bones at the posterior edge of which is the fenestra ovalis into which is inserted the footplate of the columella. Just ventral to the fenestra ovalis is a large recessus scalae tympani. Clearly visible in the dorsal aspect of the recessus scalae tympani is the perilymphatic sac as well as the processus interfenestralis.

Anterior to the fenestra ovalis and just dorsal to the anteriormost portion of the recessus scalae tympani is a vertical ridge of bone. Just anterior to this ridge is a deep foramen for the seventh cranial nerve, shared by both the hyomandibular and

School of Theoretical and Applied Science, Ramapo College, Mahwah, New Jersey, U.S.A.

palatine rami of that nerve. The palatine nerve branches from the main trunk of the facial nerve immediately upon exiting from the facial foramen and then turns anteroventrally to enter a thin bony canal, the exit of which is located at the anterior end of the basitemporal platform, medial to the point of exit of the Eustachian tube and lateral to the exit point of the palatine artery. For a portion of its length, this canal for the palatine nerve is contiguous with the canal carrying the palatine artery and thus represents a true parabasal canal. The hyomandibular ramus of the facial nerve, upon exiting its foramen, continues laterally, supported by a thin strip of bone. The hyomandibular ramus continues dorsal to the columella to the rear of the middle ear cavity, running along the lateral surface of the stapedial artery and vena capitis lateralis with which it exits from the middle ear cavity through a foramen in the lower portion of the metotic process. Just posterodorsal to the columella it gives off a thin branch, the chorda tympani which runs in an anterior direction dorsal to the columella very close to the tympanic membrane.

The vena capitis lateralis exits the middle ear as a single vessel which subsequently breaks up into individual venous branches which lower down in the neck reunite to form a single vessel. The carotid artery is found in the upper neck just below the middle ear region wrapped in a bundle of veins all of which are branches of the vena capitis lateralis. The venous bundle and its enclosed carotid artery is surrounded by a tough membrane.

The carotid artery enters the middle ear from below via a carotid foramen. The artery travels in the ventral portion of the middle ear cavity in a bony carotid canal. Approximately halfway along the length of the carotid canal is a carotid entrance foramen through which the carotid artery enters the braincase. A branch of the carotid artery, the palatine artery, continues to run forward in the parabasal canal to exit adjacent to the Eustachian tube. Just prior to entering the middle ear region from the neck the carotid artery gives off a dorsal branch, the stapedial artery. The stapedial artery enters the middle ear region through the stapedial arterial foramen in the metotic process. The foramen continues as a canal running in the same plane as the metotic process to a position just below the recessus scalae tympani. The medial wall of the stapedial arterial canal is perforated by a foramen which leads into a laterally naked canal which courses dorsolaterally to the foramen magnum. Carried in this structure is a small occipital artery. The stapedial artery continues to run first posterior then dorsal to the columella in a deeply excavated groove in the medial wall of the tympanic fossa. The anterior edge of this stapedial arterial groove forms the ventral and then the posterior edge of the recessus scalae tympani. Running lateral and dorsal to the stapedial artery is the vena capitis lateralis which leaves the middle ear cavity through the stapedial arterial foramen in the metotic process. Together the stapedial artery and vena capitis lateralis form a rete mirabile medial to the quadrate quite a distance posterior to the foramen prooticum.

The foramen prooticum is large in *Struthio* and separated from the facial foramen by a large, anteriorly directed, conical concavity, the presphenoid sinus, the anterior end of which is highly pneumatic. The foramen prooticum is found on the lateral wall at the outer surface of the presphenoid sinus. Much of the presphenoid sinus extends posterior to the foramen prooticum.

The glossopharyngeal and vagus nerves exit together from the skull via a large foramen medial to the stapedial arterial foramen. In several of the skulls studied a thin bridge of bone partially divides the vagus-glossopharyngeal foramen into regions for each of the two nerves and in one specimen (AMNH 4376) there seems to be a separate foramen for the glossopharyngeal nerve. The hypoglossal nerves exit via several small foramina located in the region between the posterior portion of the paroccipital process and the occipital condyle.

Beneath the floor of the presphenoid sinus and dorsal to the carotid foramen is the entrance to the Eustachian canal. The Eustachian tube consists of a thick hollow mambrane that is completely encased in bone in the Eustachian canal. The Eustachian tubes of both sides exit from above the basitemporal platform via a pair of widely separated foramina in the dried skull. The tube from each side runs along the ventral surface of the basipterygoid process (McDOWELL, 1948), also called by BOCK (1963) the basitemporal process, and each opens into the hind portion of the palate as a small slit located within a larger vacuity found posterior to the opening of the internal nares at the rear of the mouth.

Just anterior to the dorsal articulation of the quadrate with the paroccipital process is the upper tympanic recess from which originates a muscle mass associated with the jaw apparatus. This cavity in extending dorsally and medially fills much of the paroccipital region of the skull. At its internal end it has numerous pneumatic openings. Posterior to the dorsal quadrate-paroccipital articulation are a pair of pneumatic foramina that are not in contact with each other or any other pneumatic opening.

Conclusions

It seems difficult to avoid the conclusion that the Struthioniformes have evolved from flying ancestors. They share numerous middleear characteristics with Procellariiformes (SAIFF, 1974), Sphenisciformes (SAIFF, 1976, Pelecaniformes and Ciconiiformes (SAIFF, 1978). There are similarities in several of the foramina for the cranial nerves that open into the middle ear region, the presence and morphology of the presphenoid sinus and upper tympanic recess as well as the paths taken by the major blood vessels of the region, and the presence of a refe unirable. Not only do these orders share middle ear characters, but they also share numerous other anatomical and embryological chracteristics as reviewed by SIBLEY & AHLQUIST (1972). These include pterylosis of the wing, intestinal convolutions, hallux morphology and function, and general skull embryology.

At the same time *Struthio* retains some unique middle ear structures which clearly distinguish it from the flying forms upon which I have previously reported (SAIFF, 1974, 1976, 1978). There is the interesting arrangement of a single foramen shared by the glossopharyngeal and vagus nerves (but not always constant). There is a unique structure in the upper neck just below the middle ear for the vena capitis lateralis as well as a Eustachian tube that opens near the posterior of the middle ear and continues forward completely encased in bone to open at the rear of the palate in a manner unlike that seen in the carinates so far examined by me.

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CONVENER: F. NOTTEBOHM

Song Learning, Dialects and Auditory Templates: An Ethological Viewpoint

Peter Marler

Introduction

The next major frontiers for biological research are in the neurosciences, and one of their ultimate aims is to understand how nervous systems generate and control behavior. There is a special role for studies of avian vocal behavior giving access as they do to some of the most intricate and profound problems that neuroscientists are concerned with. Bird vocalizations include the most complex behaviors that animals perform: some are innate, and some are radically transformed through learning. There is a variety of developmental time tables from species to species, some open throughout life, others radically limited in time, so that they illustrate the phenomenon of sensitive developmental periods in almost ideal form.

The syrinx

The operation of the avian syrinx is much better understood since the work of Greenewalt (1968), supporting the "two-voice" interpretation. The songbird vocal tract does not operate by modulation of resonant air cavities as in human voice production. It is actively driven by the syringeal membranes, as George Hirsch (1966) confirmed by showing that several songbirds vocalizing in helium air showed no pitch change. Much remains to be learned about how the two voices operate, and about the relative contributions of the intrinsic syringeal musculature and the general respiratory musculature in the dynamics of oscine sound production.

Song dialects: their perceptual and genetic significance

Song dialects have been well studied in the White-crowned Sparrow (Marler & Tamura 1962; Baptista, 1975). Baker has demonstrated both genetic differences across a local dialect boundary, and also an influence on the settling patterns of young birds, showing that they are deflected in favor of the dialect of the birth place, if born near a boundary (Baker, 1976; Baker & Mewaldt, 1978). In other species the distribution of song variants is clearly much more complex, as Kroodsma (1974) has shown in the Bewick's Wren. Some of a male's 16 or so songs are shared with the father, while others are acquired after dispersal from the birth place. There may be some conflict between advantages to staying home and matching the father's song, and to moving away, and possessing songs that match those of new neighbors. Indeed it is becoming increasingly clear that a variety of selection pressures impinge on dialects and on the nature and size of the song repertoire.

The nature and physiological basis of the varying salience of biologically-significant sound stimuli is another basic neurobiological theme. Playback studies suggest that dialects in a song or call affect its salience as a stimulus to other individuals. The perceptual significant of variations in repertoire size or quality is an active issue. Perhaps females are

Rockefeller University, New York, N. Y., U.S.A.

responsive to such variations, and find large repertoires more stimulating than small ones? Kroodsma (1976) prepared two versions of a long sequence of canary song, one unmodified, the other simplified by deleting all but five of the 30 or so syllable types and closing up the gaps. Played to females, this simplification slows down the rate of nest building evoked by the song, delays the laying of the first egg, and reduces the overall number of eggs laid. It remains to be seen whether the more subtle variations that occur in nature will also differ measurably in their effect on females, and whether they correlate in turn with the fitness of a male as a potential mate.

Nowhere else in the animal kingdom do we find learning playing as dominant and complex a role in the development of behavior as in bird vocalizations. The only remote parallel is in speech development in children. Two themes of particular interest to neurobiologists are the existence of sensitive developmental periods of life, in which the organism is especially responsive to stimulation, and secondly the phenomenon of selectivity in such responsiveness, with young birds having to learn their songs and yet possessing the ability to select a particular set of sounds, including songs of the species, as a focus for the learning process.

Sensitive periods

We have known for some time that several songbirds learn song during a quite short period in youth, then become refractory to any further influence on their own motor patterns of singing and finally produce their own rendition of the songs from memory. However the details vary from species to species. In early studies we defined the sensitive period crudely by presenting song playback at different periods of life to birds in the laboratory (Thorpe, 1958, Marler & Tamura, 1964, Marler, 1970). Some learned and some did not, developing the innate song instead. But of course in nature a bird is presented with a changing sequence of potential models as it matures. Immelmann (1969) confronted Zebra Finches with such choices in characterizing their rather sharply-defined sensitive period for song learning.

Kroodsma (1978) has shown how we can refine the definition of sensitive periods in ways that illuminate the role in dispersal. Beginning at one or two weeks of age, young male Long-billed Marsh Wrens were exposed over a 72 day period with a total of 44 different song types, some presented over 9-day periods, some over 6-day periods and some for only three days. In every case a thousand exposures constituted one day's treatment for a given song. The 9-day exposures serve for a rough definition of the sensitive period, and the 3-day one for finer resolution, showing that while learning occurs roughly between 15 and 60 days of age, there are suggestions of two peaks of sensitivity. This is especially interesting in view of Kroodma's early work on song learning in Bewick's Wrens in the wild, suggesting that learning both before and after dispersal from the home area may be important in the life of wrens.

We have probably underestimated the potential flexibility of song learning programs. While much previous work on song learning had used emberizine and estrildine finches as subjects, the Canary is a cardueline finch. I was surprised to find that male Canaries which had been prevented from hearing their own voice for the first 200 days or so of life by masking noise, with a song like that of deafened birds when the noise was turned off in mid-breeding season, achieved no improvement for the rest of that season, but were able

to achieve a much more normal song in the breeding season that followed, in their second year of life (Marler & Waser, 1976). It now appears that male Canaries continue to modify their songs throughout life, as Nottebohm & Nottebohm (1978) have recently documented by comparing the songs of male Canaries in the first and second year. Not only are many song syllables replaced by others, but there is also a significant increase in the song syllable repertoire size. Thus in some birds the complexity of the song repertoire may serve as a kind of age marker, permitting females to be more selective in mating with the most fit mates that are available to them (Nottebohm 1972). It begins to look as though adult song plasticity is a particular feature of cardueline finches, for Güttinger (1974, 1976) has recently found evidence of adult song change in the European Greenfinch. Call plasticity has also been described in siskins, the Twite and in crossbills and the Pine Grosbeak, in some cases throughout life (Mundinger, 1971; Marler & Mundinger, 1975; Adkisson, in press). This seems to be lacking from the closely related sparrows. These variations in developmental plasticity in closely related species are ideal subjects for physiological study.

Selective Imitation

Similarly on the issue of selective imitation of certain models, some species are relatively indiscriminate – interspecific mimics are obvious cases. Experiments have shown that where the breadth of acceptable models is greater under experimental than natural conditions, the limitations are sometimes social rather than auditory. Nicolai's (1959) Bullfinches and Immelmann's (1969) Zebra Finches are cases in point where learning is guided within a social framework, the young male learning sounds emanating from the father. But in other cases a young male learns selectively from a loudspeaker. Thorpe (1958) demonstrated such selectivity in his classic studies of song learning in the Chaffinch, and we found that male White-crowned Sparrows accept conspecific song and reject Song Sparrow song. We have recently found another case in the Swamp Sparrow, *Melospiza georgiana* (Marler & Peters, 1977).

The normal songs of the Song and Swamp Sparrows, although similar in duration, are very different in temporal organization. Swamp Sparrow song is simple, consisting of a slow trill of similar slurred notes. That of the Song Sparrow is more complex, with several distinct parts, several different note and syllable types, and a trill near the end. Both engage in vocal learning, and in both songs of socially-isolated males are significantly abnormal, with simpler syllables and fewer component parts. We designed an experiment to present young male Swamp Sparrows with songs of both species to see if selective learning would occur, and to try to specify some of the acoustic parameters involved. For this purpose, we created a series of artificial songs. Distinctively different syllables were edited out from tape recordings of nocmal local songs of the two species. These were then spliced together in a variety of simple temporal patterns. Some were "Swamp-Sparrow-like" sequences of indentical syllables at various steady rates. "Song-Sparrow-like" patterns included variable rates of delivery, such as accelerating or decelerating series, and a multi-partite structure – in this case two parts rather than just one.

Our expectation was that the pattern differences would provide the basis for any selectivity. It seemed unlikely that individual syllables would be important in species recognition because of the great intraspecific variability in syllable form. However as a

precaution, we created a double set of the ten patterns, one composed of 16 different Swamp Sparrow syllables, the other from 16 different Song Sparrow syllables. These were all selected to be sufficiently distinct that if imitation occurred we would be able to determine from which pattern they had been selected. Male Swamp Sparrows were played these tapes twice a day in morning and evening for 30 days, between 20 and 50 days of age. We already knew this to include the sensitive period for vocal learning in Swamp Sparrows. In the first year we worked with birds taken as nestlings from wild nests, and in the second year with birds hatched from eggs placed under Canaries. The results were the same. Many songs were copied, but every one was composed of Swamp Sparrow syllables. Although there was equal exposure to Song Sparrow syllables, in identical patterns of temporal organization, none of these were copied. Thus the male Swamp Sparrow exhibits innately, selective vocal learning, accepting only conspecific syllables for imitation, and rejecting Song Sparrow syllables. The choice was clearly made at the level of the components from which the song was constructed and not the overall pattern.

Auditory Templates

This finding also helps to fill a gap in a hypothesis we have been developing that explains song learning in some species in terms of innate but modifiable auditory templates. Building on KONISHI's (1965) discovery that early deafening erases many species specific song features, we began thinking of a kind of innate auditory filter that would help a young male to focus attention on conspecific models. In listening to them the filter would become modified and refined as the vehicle for the memory trace or engram of what has been learned. Then the bird would begin to sing, using the memory trace as a template to guide vocal development. A deaf bird can't do this so you get a very simple song. An intact bird does better and this presumably tells us something about the specifications of the innate template.

One of several gaps is our ignorance of how much has to be postulated as innate? Should we think in terms of something like an innate mental image of a song, imperfect but still an adequate skeleton on which to put the flesh of normal song? The Swamp Sparrow experiment suggests not. I now prefer to think in terms of innate responsiveness to a very elementary property of conspecific song, sufficient to reject certain competing sounds but leaving plenty of latitude for subsequent learning. I wonder if many releasers that ethologists have studied in young birds may not be better thought of as learning guides than as innate equipment that is ready made for adult use (MARLER, 1977).

There is evidence that human babies possess some innate guidelines in the selection of features of speech on which they should first focus their attention in trying to classify speech sounds and attach meanings to them.

Conclusion

The number of parallels between vocal learning in birds and in man is striking enough that we no longer need feel hesitant in suggesting that the principles involved are widely applicable. They bear on neurobiological principles that recur in widely different organisms – even though they may be put to different behavioral functions (MARLER, 1975, in press). Comparative ethological studies of vocal development in birds and man

document several phenomena that invite physiological investigation. These include the existence of sensitive periods, narrowly defined in some species and broadly defined in others. There is selectivity in the learning process, such that the young organism is differentially responsive to certain patterns of sound rather than others, even though such predispositions may be modifiable as a result of subsequent experience. These phenomena are manifest in patterns of motor behavior that offer a wide spectrum of complexity, some simple, others enormously complex, inviting comparison with the most elaborate motor skills that we know of. Many neurobiologists are now concerned with a search for animal analogues to issues that fascinate us in study of the human brain and physiological correlates of thought and consciousness. I would venture the suggestion that birds may prove more suitable as models than some of the traditional mammalian subjects, as I believe will be evident from some other contributions to this symposium.

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Neural Pathways for Song Control: A Good Place to Study Sexual Dimorphism, Hormonal Influences, Hemispheric Dominance and Learning

FERNANDO NOTTEBOHM

Introduction

Chaffinches, White-crowned Sparrows, Zebra Finches and many other oscine songbirds learn their song by imitating conspecifics (THORPE, 1958; MARLER, 1970 and this symposium; IMMELMANN, 1969). Such vocal learning requires three different kinds of processes: 1) choice of a correct model; 2) remembering this model; 3) modification of vocal output until the auditory feedback it generates matches the model (KONISHI, 1965). This is an interesting situation for a neuroethologist because it affords the opportunity to study brain pathways involved in each of these tasks.

The vocal organ of birds

The syrinx is the vocal organ of birds. In oscine songbirds it consists of two functionally equivalent halves. Each half has its own air supply, sound source, muscular control and innervation. Sounds are produced by the periodic oscillations of the internal tympaniform membranes (i.t.m.). There is one i.t.m. in each syringeal half, forming the medial wall of the upper reaches of each bronchus. The i.t.m. are drawn into the bronchus as a result of the Bernouilli effect, periodically interrupting air flow. This pattern of oscillation is presumably in phase with turbulence generated as air flows by the narrow opening connecting bronchus and trachea. The syringeal muscles modulate the sounds produced by setting membrane tension and controlling airflow past them. Each syringeal half is innervated by the tracheosyringeal branch of the ipsilateral hypoglossus nerve. This topic is reviewed in greater detail elsewhere (NOTTEBOHM, 1975).

Left hypoglossal dominance

Both syringeal halves are anatomically symmetrical, and yet most vocal sounds are produced by the left half, only a few by the right one. This can be demonstrated by cutting the right or left tracheosyringealis nerve. In Chaffinches, White-crowned Sparrows, White-throated Sparrows and Canaries section of the left tracheosyringealis results in loss of a majority of song components, which are replaced by silent gaps or by other, poorly modulated sounds. Section of the right tracheosyringealis results in the loss of a few sounds, if any (NOTTEBOHM, 1971, 1972; NOTTEBOHM & NOTTEBOHM, 1976; LEMON, 1973). Left hypoglossal dominance for vocal control is accompanied by a somewhat more robust musculature on the left syringeal half. Left hypoglossal dominance is not likely to be determined by peripheral restrictions on what each syringeal half and its corresponding innervation can do. Section of the left hypoglossus in young Chaffinches and Canaries is followed by atrophy of the left syringeal musculature; in such birds normal song develops under dominant right hypoglossal control. (NOTTEBOHM, 1971; NOTTEBOHM & NOTTEBOHM, 1976).

The Rockefeller University, New York, N. Y., U.S.A.

Chaffinches develop their song during their first year of life. In this species reversal of left hypoglossal dominance is possible only up to the time when song starts to crystallize into the stable adult pattern. Canaries modify their song repertoire as they go from year 1 to year 2 to year 3 (NOTTEBOHM & NOTTEBOHM, 1978 and unpublished observations), and in this species reversal of left hypoglossal dominance is possible in adulthood (NOTTEBOHM, in press). Thus the plasticity required for vocal learning seems to be related to the plasticity required for reversal of hypoglossal dominance.

Brain pathways for vocal control

Experimental work with Canaries has uncovered a number of discrete brain areas involved in vocal control (NOTTEBOHM, STOKES & LEONARD, 1976). Of these, the highest vocal control station is the hyperstriatum ventrale, pars caudale, HVc. HVc projects to the robust nucleus of the archiastriatum, RA, which in turn sends a direct pathway to the caudal half of the hypoglossal nucleus, nXIIts. Motor neurons in nXIIts innervate the syringeal musculature via the tracheosyringeal branch of the hypoglossus (Figure 1). This innervation too is strictly ipsilateral. We do not know yet at what level the right and left efferent pathways integrate their output.

Left hemispheric dominance and dominance reversal

A canary that has suffered bilateral destruction of HVc is rendered aphonic. He adopts the stance and dynamics of singing behavior, but not a sound is to be heard, as if the syrinx has been disengaged. Such a bird does not recover its voice even one year later. By contrast, unilateral lesions of HVc have very dissimilar effects, depending on side affected. Lesions of left HVc have a profoundly disorganizing effect on the song of adult Canaries: virtually all syllable types and phrase structure are lost. Comparable lesions of right HVc tend to spare a good many of the syllables and leave phrase structure intact. This right-left

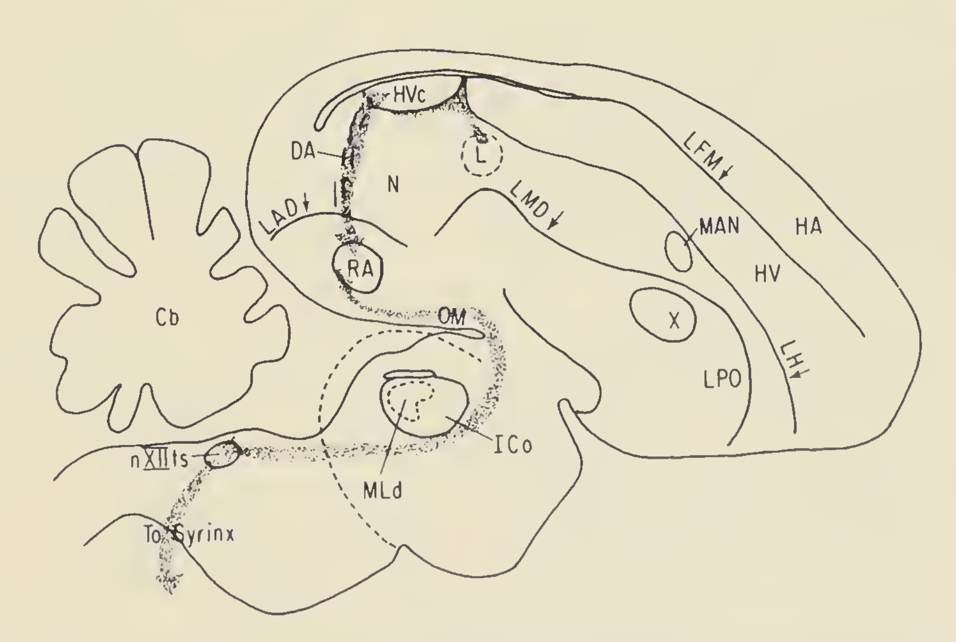


FIGURE 1. Schematic drawing of the saggital section of a Canary brain showing relations between the auditory projection of caudal neostriatum (field L) and stations of the efferent pathway controlling song. Area X of the lobus parolfactorius receives a heavy projection (not shown here) from HVc, suggesting that the function of area X is somehow related to vocal behavior (modified from KELLEY & NOTTEBOHM, in press).

difference is also reflected in unilateral lesions to RA (NOTTEBOHM, STOKES & LEONARD, 1976).

Canaries that lost their left HVc as adults are able to develop a new song repertoire under right HVc and right hypoglossal control. When early section of the left tracheosyringealis leads to right hypoglossal dominance, the right HVc is dominant too. In such birds, lesions of the right HVc has the same effect on song as lesion of the left one in otherwise intact birds (NOTTEBOHM, 1977).

Interfacing with auditory pathways

Vocal learning in songbirds relies on auditory information. Clearly, efferent pathways controlling song must have access to auditory information, and this is so. Field L, the telencephalic auditory projection sends a massive projection of fibers to a shelf of tissue closely opposed to the ventral margin of HVc (Figure 1). We do not know yet if this projection is required for vocal learning (KELLEY & NOTTEBOHM, in press).

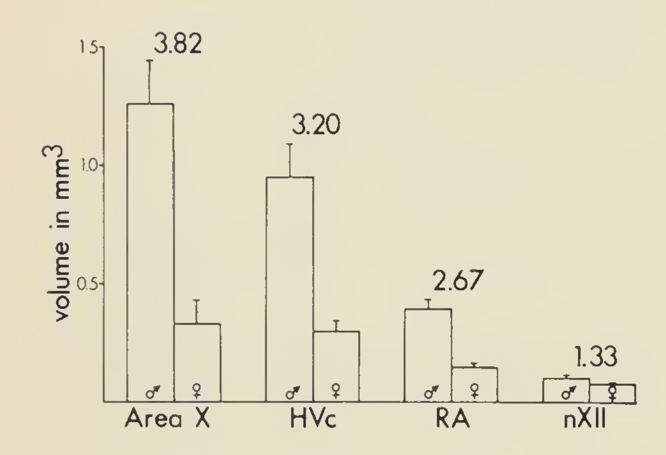


FIGURE 2. Volumes occupied by four neural regions associated with vocal behavior in male (N=5) and female (N=5) Canaries. Each bar represents the mean of the total (right plus left) volumes of each area sampled, and the vertical line above the bar is the standard deviation of the individual values. The ratio of the male to the female mean is given for each region (modified from NOTTEBOHM & ARNOLD, 1976).

Sexual dimorphism

In most songbirds males assume the major responsibility for territorial defense and sexual advertisement and it is in males that song is particularly well developed. Whereas adult male Canaries have complex songs with 20–40 different syllable types, female Canaries do not normally produce adult male-type song. When adult female Canaries treated with testosterone sing the loud, stable song typical of males, they include in their song only a meagre repertoire of 4 or 5 different syllable types. A similar situation occurs in Zebra Finches, with the difference that in this species testosterone treatment of females does not yield song. Such sexual dimorphism in behavior is mirrored in the efferent pathways controlling song (Figure 2). In Canaries and Zebra Finches HVc and RA are several times larger in males than in females, and this difference is more accentuated in Zebra Finches than in Canaries. These anatomical differences between the sexes may be expected to reverberate through other brain systems not directly related to song. Area X of lobus parolfactorius, which receives a projection from HVc is large and clearly recognizable in male Zebra Finches, yet not recognizable at all in females (NOTTEBOHM & ARNOLD, 1976). This anatomical dimorphism of the brain may of course reflect a variety of influences. Not only are males and females genetically different, but they have been exposed to different hormonal regimes and experiences. The contribution of each of these variables to the observed dimorphism still remains to be determined.

The influence of testosterone on song

Male songbirds develop song under the influence of testosterone. So, for example, male Chaffinches normally acquire their adult song when 9–11 months old, but can be induced to do so at 6 months of age if at that time they are treated with testosterone (THORPE, 1958). Conversely, the onset of spring song in Chaffinches can be delayed by castration at 6 months. If such a bird then receives testosterone at 2 years of age, well after the end of the critical period for song learning, it will develop a song that matches a tutor presented at that time (NOTTEBOHM, 1960).

Male Canaries castrated 1–3 weeks after hatching develop subsong and varying degrees of plastic song, but at 7 or 8 months of age become silent and for the duration of that first breeding season sing little if at all, in marked contrast with the profuse song of intact males of similar age. This observation is interesting because it suggests that whereas subsong and plastic song can develop in a first year bird in the absence of testosterone, adult song is much more dependent on this hormone (unpublished obs.).

In Zebra Finches normal song develops in intact males as well as in males castrated soon after hatching (ARNOLD, 1975 a). However, the amount of singing done by early castrates or by birds castrated as adults is very much dependent on the presence of testosterone. In this species castration reduced the rate of singing and tempo of song, though it does not affect the structure of song syllables (PRÖVE, 1974; ARNOLD, 1975 b).

The syrinx and its innervation may be one place where testosterone exerts its effect on song. The size of syringeal muscles is markedly smaller in intact male Zebra Finches than in castrates (ARNOLD, 1974). Motorneurons innervating these same syringeal muscles concentrate radioactive label following systemic injections of tritiated testosterone (ARNOLD, NOTTEBOHM & PFAFF, 1976). This latter observation was unexpected. Until then testosterone had been usually credited with exerting its neural effects by acting at higher brain stations, such as the hypothalamus, and its role in such higher brain stations is likely to be very important in triggering behavior. But what could be the significance of testosterone sensitivity in motorneurons? I hypothesized that its role there was one of regulating neurotransmitter synthesis, so that pathways which under testosterone (T) influence received more signal traffic would be able to match this traffic with neurotransmitter availability. As will be seen below, this hypothesis was correct in focusing attention on neurotransmitter related processes, though possibly wrong in the exact mechanism it postulated.

The neurotransmitter used by the motorneurons innervervating the syrinx is acetylcholine. In joint research with VICTORIA LUINE (in prep.), we looked at the effects of T on the levels of two enzymes: choline acetylase (CAT), responsible for acetylcholine synthesis; and acetylcholinesterase (AChE), responsible for decoupling the acetyl and choline moities soon after released into the neuromuscular synaptic cleft, thus ensuring that synaptic transmission is narrowly defined in time. Though we are still unclear about the variables affecting CAT levels, we now have strong evidence that the levels of AChE are T dependent. Four weeks after castration the levels of AChE in the syrinx of Zebra Finch males are approximately one half those in intacts. This difference is completely corrected by testosterone therapy. Interestingly, a comparison of the levels of AChE in the left and right halves of the syrinx of Canary males indicates that whereas the left has $894 \pm 63\ 10^{-9}$ M of AChE, the right side has $592 \pm 52\ 10^{-9}$ M, a significant difference of 34% (n

= 10). This difference in the levels of AChE between the two sides disappears following castration, the left and right syringeal halves showing, respectively, 286 ± 33 and 256 ± 33 10^{-9} M of AChE.

We do not yet know wether the effects of T on AChE result from direct effects of T on syringeal muscle or motorneurons. Joint work with IVAN LIEBERBURG (in prep.) indicates that the syrinx itself has an unusually high concentration of T-specific receptors. The presence of high affinity T receptors in the syrinx, the occurrence of T dependent changes in AChE activity in syringeal muscle, and the concentration of label in the nucleus of hypoglossal motorneurons following ^{3}H-T systemic injections suggest T acts on both muscle and motorneuron via classic genomic mechanisms. The difference in AChE levels between the right and left syringeal halves suggests that on top of these genomic effects there may also be an effect of use and disuse, as suggested also by right-left differences in muscle mass. The problem ahead is to tease appart and understand these interactions between use and disuse and genomic effectiveness of T.

Conclusion

This review has highlighted some aspects of recent work on the neureothology of birdsong. It has been my purpose to emphasize a progression of steps, from the behavioral problems themselves – selectivity in song learning; occurrence of motor learning; hemispheric dominance; critical periods for song learning; sex dependent song learning – to the brain pathways controlling vocal behavior, finally to molecular events related to the manifestion of song. The relation between information at these various levels is still disappointingly indirect, but the path to follow seems open and full of promise. The greatest challenge, perhaps, is to identify and relate neural changes induced by hormone effects, by use and disuse and by learning. The vocal control pathways of the songbird brain seem propitious material!

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Anatomical and Electrophysiological Studies of Sexual Dimorphism in a Passerine Vocal Control System

Arthur P. Arnold

Song in passerine birds is often the prerogative of the male and is frequently associated with other reproductive behaviors. Females sing little or not at all in some species. The experiments reviewed in this paper were undertaken to determine the physiological processes which underlie this difference in behavior.

Zebra Finches *(Poephila guttata)* were selected as a convenient laboratory species. Male Zebra Finches sing a quiet courtship song which is frequently directed at the female. Females do not sing. Castration of males substantially reduces the numbers of songs sung but does not abolish song (Arnold, 1974, 1975; Pröve, 1974) and replacement therapy with injections of testosterone propionate reverses the effects of castration. However, females cannot be induced to sing, even when implanted or injected with testosterone propionate at doses which are effective in restoring full singing in castrate males (Arnold, 1974 and unpublished.)

In order to determine the physiological basis for the sexual difference in behavior, one must have some knowledge of the neural and hormonal basis for song in the male. Nottebohm and his colleagues have discovered a series of anatomically discrete regions in the brain of Canaries *(Serinus canarius)* which form the main portion of the song control system (Nottebohm, et al. 1976). Lesions in several of these areas produce deficits in song, and these regions are interconnected and have a descending projection to the motoneurons controlling the syrinx (summarized schematically in Figure 1). The caudal nucleus of the hyperstriatum ventrale (HVc) projects to the robust nucleus (RA) of the archistriatum, which in turn projects to the syringeal motoneurons (nXIIts). HVc also projects to Area X of the lobus parolfactorius, and RA sends axons to synapse in nucleus intercollicularis (ICo) in the midbrain. Stimulation of ICo in many bird species elicits vocalization (e.g. Phillips & Peek, 1975). Recently, anatomical evidence reveals projections of the magnocellular nucleus of the neostriatum (MAN) to both HVc and RA (Nottebohm & Kelley, 1978 in press, not shown in Figure 1).

Zebra Finches also possess all of these neuronal regions, and electrophysiological experiments indicate that they project directly or indirectly to the motoneurons controlling the syrinx. In these experiments, I recorded electromyographic (EMG) responses in the ventral intrinsic syringeal muscles while stimulating in the brain with trains of 0.3 millisecond cathodal pulses at 500 Hertz, using small, glass-insulated tungsten microelectrodes. Such microstimulation allows fine grained localization of sites which are involved in control of syringeal muscles. Very low threshold stimulation in HVc, RA, and Area X, produces contraction of the ipsilateral syringeal muscles. For example, stimulation of right or left HVc with a train of four pulses evokes ipsilateral syringeal EMG responses at thresholds a low as 1.0 microampere or less (latencies about 20–25 milliseconds). Minimum thresholds in other areas were at least as low as 5 microamperes. Since these currents activate extremely limited regions of neural tissue, this suggests a dense indirect

Department of Psychology and Brain Research Institute, University of California, Los Angeles, California, U.S.A.

projection from these areas to the ipsilateral syringeal muscles. Contralateral EMG responses were occasionally observed in response to higher threshold stimulation, at about 5–20 times threshold for the ipsilateral response, suggesting a much less dense contralateral projection.

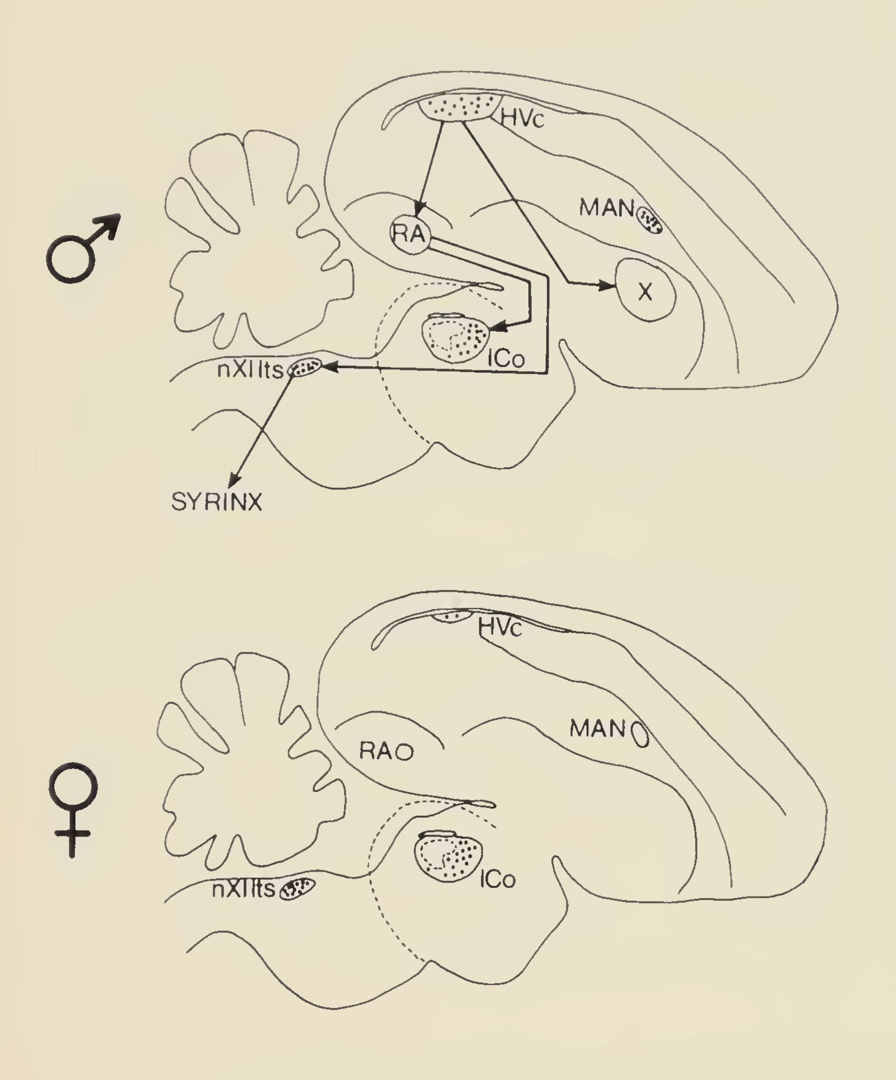


Figure 1. Brain regions involved in song control are shown schematically together with the pattern of anatomical projections (arrows) discovered in the Canary by Nottebohm et al. (1976). Black dots indicate the presence of cells which concentrate testosterone or its metabolites in the Zebra Finch (Arnold et al., 1976; Arnold & Saltiel, in preparation). The number of dots is not necessarily proportional to the number of hormone-concentrating cells in each area, but is meant to indicate presence or absence of labelled cells. A cell is considered to be labelled if the number of silver grains over the cell body reaches a criterion of five times the density over adjacent neuropil. Since the accumulation of radioactivity in female MAN did not reach this criterion, no labelled cells are indicated.

Since song in Zebra Finches is affected by androgens secreted by the testis, it would seem likely that the effects of androgen on song might be mediated, at least in part, by androgen influences on neurons which control song. There is now a large literature on mammals and other vertebrates which indicates that steroid hormones are accumulated specifically by cells in brain regions involved in behavioral and neuroendocrine events which are mediated by the hormone in question (e.g., McEwen, et al. 1974). The autoradiographic method allows one to localize such cells. It is quite likely that the function of neurons which selectively accumulate the hormone is altered by the hormone, and thus the autoradiographic method is a logical first step to determine where androgens act to influence song. We used this method with injections of radioactive testosterone into castrated adult male Zebra Finches (Arnold et al. 1976). Testosterone or its metabolites were accumulated in neurons in MAN, HVc, ICo, and the syringeal motor nucleus (nXIIts) (Figure 1). The labelling of these cells is blocked by preinjection with non-radioactive testosterone, thus demonstrating that the accumulation mechanism is of limited capacity (Arnold, unpublished). Other areas of the brain containing hormone-concentrating cells were the medial preoptic area, periventricular magnocellular nucleus of the

anterior hypothalamus, the infundibular region of the posterior hypothalamus, and the lateral septum. The possible involvement of these other neural regions in song control cannot be excluded, especially in light of the implication of the preoptic area and anterior hypothalamus in courtship behavior in other avian and vertebrate species (Hutchison, 1976).

Several aspects of these autoradiographic data are worth emphasizing. First of all, these data imply that steroid hormones do not bring about a change in behavior by acting at one or two restricted brain areas. Rather, it would appear that they may act at many levels in the song control network, possibly producing selective changes at each, to modulate singing behavior. Secondly, the concentration of hormone by the syringeal motoneurons suggests that at least part of androgen's effect on singing is exerted by alterations in the function of the final common path, through which all descending neuronal elements exert their effects on song. This raises the intriguing question of how these motoneuronal effects can exist and yet only alter certain parameters in the behavior. Finally, the accumulation of hormone by cells in telencephalic song areas (MAN, HVc) is not predicted by the phylogenetically conservative pattern of steroid accumulation in limbic areas of other vertebrates (Morrell et al. 1975).

The autoradiographic experiments suggest that androgens act centrally, on the brain, to exert some influences on song, but it is also important to consider the possibility that they might have important peripheral actions, for example on the syrinx. This appears to be the case. Castration of adult males causes a substantial decrease in the size of syringeal muscles, and androgen replacement reverses this decline (Arnold, 1974). Autoradiographic experiments show accumulation of testosterone or its metabolites by syringeal muscles (Arnold, in preparation). Therefore, it is likely that androgens have a direct effect on the syrinx. This conclusion further substantiates the view that androgenic influences on song are exerted at many levels (both neural and muscular) in the song control system.

To explain the difference in vocal behavior between male and female Zebra Finches, we have looked for various anatomical and physiological differences between the sexes. The most striking difference was reported by Nottebohm & Arnold (1976). Five neural regions thought to be related to song control (HVc, RA, Area X, and nXIIts) are markedly smaller in volume in female Zebra Finches than in males. This suggested that the female's inability to sing was a result of the small size of the brain regions controlling song. This suggestion is strengthened when one considers the sexual difference in volume of song regions in Canaries. Female Canaries are unlike female Zebra Finches in that they do sing when given androgens. The volumes of their song areas are correspondingly larger (when expressed as a percentage of the size of male song areas) than those of female Zebra Finches. Thus the ability to sing and volume of song areas are correlated.

Is the sexual dimorphism in volume of these brain areas a result of sex differences in circulating hormone levels, or is it independent of these, suggesting an irreversible sexual difference which might be determined early in development? To evaluate the first part of this question, I compared volumes of song areas in intact and castrate adult male Zebra Finches, and in intact females and females injected with large doses (200 microgram per day) of testosterone propionate for three weeks. Castration did not reduce the volume of song areas in males, nor did androgen administration change the volumes in females.

Is the vast difference in size of these areas also accompanied by differences in function, or are the female areas just smaller equivalents of the male areas? Electrophysiological experiments show that microstimulation in HVc in females also elicits ipsilateral syringeal contractions, so that this area does have indirect projections to the syringeal muscles as in the male. However, the parameters of stimulation are different. Longer pulse trains are required to produce a response (for minimum thresholds one needs to apply 4–5 pulses in the male, and about 10 pulses in the female at the stimulation parameters indicated above), thresholds are typically higher in females, and the latency of response is longer (about 30–40 milliseconds). These differences indicate that although there is a pathway between the female HVc and syrinx, definite functional differences exist between the female and male HVc.

In addition to these anatomical and functional differences in the male and female brain, there appears to be a sex difference in the sensitivity of some neurons to hormones, as implied by autoradiographic evidence. After injection of radioactive testosterone into adult ovariectomized females, one sees accumulation of hormone in only some of the same neural regions as in males (Arnold & Saltiel, in preparation). In ICo and the syringeal motoneurons, the distributions of labelled cells is comparable to that in males. Similarly, in some areas outside the song control network per se (preotic area, periventricular magnocellular nucleus of the hypothalamus, infundibular region), the pattern of labelled cells is similar in males and females. But in two song regions, HVc and MAN, there is less accumulation in females. In female HVc, only an occasional labelled cell is seen, and this may well reflect the very small size of this nucleus in females. There are likely to be many fewer cells in the female HVc in general, and hence many fewer hormone-concentrating cells. In the female MAN, cells accumulate only small amounts of radioactivity, in marked contrast to the rather heavily labelled cells in the male (Figure 1). There is a difference in the amount of hormone accumulated per cell, and this cannot be a simple reflection of a general absence of MAN cells in the female. Rather, it suggests that some aspect of the hormone accumulation process in cells of MAN differs in the two sexes. It could be argued that the sex difference may not be specific to MAN cells, since (for example) a general sex difference in the accessibility of the brain to the circulating hormones could account for a lack of accumulation in females. However, this is an unlikely explanation, since the hormone reaches other brain regions (ICo, nXIIts, etc.) and is accumulated in comparable fashion in both males and females. Thus, the sex difference is in accumulation in MAN relative to other brain regions.

Besides the various sex differences in brain, there is also a sexual dimorphism in syringeal structure. Syringeal dimorphisms exist in a number of avian species (Häcker, 1900; Warner, 1971). In female Zebra Finches, the intrinsic syringeal muscles are much thinner than those in males (Arnold, 1974). Administration of androgens causes the female syringeal muscles to grow, but they do not attain the size of males'. Therefore it appears that sexual differentiation of the song control system is not limited to the neural level.

We do not know yet what factors during development of Zebra Finches are responsible for the sexual differentiation of the brain and syrinx. In domestic ducks, syringeal morphology is affected by the presence or absence of the ovary during embryonic development (Witschi, 1961). Similarly there is evidence that sexual differences in

behavior of quail are determined by organizational effects of gonadal steroids during embryonic growth (ADKINS, 1975). Whether the sexual differences in the vocal control system of Zebra Finches are similarly determined is an interesting question for future study.

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Functional Lateralisation in the Chicken Fore-Brain Revealed by Cycloheximide Treatment

Lesley J. Rogers

Introduction

Hemispheric specialisation was first identified in the human brain, where speech was found to be located in the left cerebral hemisphere (see Geschwind, 1974). Subsequent studies on split-brain patients and subjects tested after injection of an anaesthetic into one or other of the two carotid arteries demonstrated functional lateralisation of many other behaviours in the human brain (Bogen & Gazzaniga, 1965; Bogen & Gordon, 1971). To put it simply, in most people the left hemisphere talks, writes, performs mathematical calculations, and thinks in a logical, serial manner, while the right hemisphere recognises shapes and faces, appreciates music, and is more concerned with nonverbal ideation.

Lateralisation was thought to have developed as a concomitant of language, still believed by many to be a purely human attribute. While there is considerable information about lateralised brain function in humans, until recently no equally convincing evidence for lateralisation was available for any other species. This was presumably because its demonstration requires sensitive behavioural tests.

But functional lateralisation has now been found in the avian brain. Nottebohm (1977) has shown that the left hemisphere of Canaries exerts a dominant control over vocal behaviour. Although there has been speculation about the similarities between language and bird-song, the left side localisation described for humans and Canaries may be coincidental. However, the very fact that such unilateral specialisation exists leads one to question whether it is associated only with language and song, or wheather it is a more common phenomenon, both with respect to the number of species in which it occurs and the number of different behaviours which are lateralised. It has been possible to demonstrate that a number of behaviours in young domestic fowl chicks are controlled more effectively by one hemisphere than by the other. The relevant experiments, which used the drug cycloheximide to modify brain function, are reviewed in this chapter.

Cycloheximide's effects on behaviour

First, it is necessary to explain how the drug affects behaviour. Cycloheximide is an antibiotic which blocks mammalian ribosomal protein synthesis. Its use previously demonstrated the protein basis of long-term memory formation (Mark & Watts, 1971), and more recently, it has been found to affect other behaviours. When administered intracranially to chickens in their first week of post-hatched life, not only did it block long-term memory formation of events occurring around the time of injection, but it also permanently rendered the chicks incapable of learning at their normal rate. It has now been well established that, if a single 20 μg dose of cycloheximide in 25 μl of sterile 0.9% saline is administered into each side of the chicken fore-brain at any time between days 2 and 10 of life, the rate of learning a visual discrimination task and a visual habituation task will be

Department of Pharmacology, Monash University, Clayton, Victoria 3168, Australia

significantly slower than that found for control animals treated with saline alone. The same dose of cycloheximide also slows learning of an auditory habituation task, but the sensitive period for this occurs at an earlier time, from immediately after hatching to day 3 of life (Rogers et al., 1974).

The visual discrimination learning task requires a chick, deprived of food for 3 hours, to search for grains of chick mash scattered randomly over a background of small pebbles, which have been stuck down to the floor. The grains differ from the pebbles in brightness and texture, but not in their ranges of shape, colour or size. Pecking commences without discrimination being made between grain and pebbles. The choice of each peck is scored by observation, and the numbers of errors in each of three blocks of 20 pecks are used to generate a learning curve. Within the total number of 60 pecks allowed, control chicks learn to discriminate grain from pebbles. By the last block of 20 pecks a control group makes a mean of 2 or 3 errors, while a group which has received cycloheximide still makes a mean of 10 errors. Thus, the number of errors in the last 20 pecks can be taken as a measure of learning rate. The test was applied to groups of animals injected on day 2 after hatching and tested at ages ranging from 5 days to 20 weeks; in the cycloheximide-treated animals the same amount of learning retardation was found to be present at these various ages. Cycloheximide slows learning rate, but it does not prevent learning. If treated animals are allowed more experience on pecking discrimination, eventually their performance will reach a criterion equal to that of controls. Thereafter they can perform this discrimination under various reduced light intensities as well as can control groups. This suggests that the defect is in learning, rather than visual perception.

Visual habituation rate is measured by placing a novel visual stimulus (a torch battery) in the home cage, and scoring the amount of time the chick spends silently fixating it on each of four successive presentations. The visual fixation is made using the lateral field of vision. The end of the fixation period is marked by rapid moving away from the frightening novel stimulus, usually jumping to escape from the home cage containing it. Control animals show a decreasing amount of fixation time with each presentation, and, by the fourth presentation, are found to fixate the stimulus for significantly less time than are the cycloheximide-treated animals. The mean fixation times for the fourth presentation in such an experiment were 10 $\pm$ 3 seconds for controls and 29 $\pm$ 6 seconds for a treated group ($.002 < P < .02$, 2-tailed Mann-Whitney U test).

Control chickens, tested for auditory habituation in the second week of life, cease to orient to an auditory stimulus (a banging sound) after about 4–7 presentations. Cycloheximide treatment markedly delays habituation of the response which persists for 2 to 3 times as many presentations. These effects of cycloheximide on auditory and visual learning are found to be still present in adulthood.

In addition to its effect on learning, cycloheximide alters attention, such that there is less switching of attention from one stimulus to another. A similar state of 'attentional persistence' is produced by testosterone treatment (Rogers, 1974). One way to measure it is to record pecking for red and yellow food grains scattered over a background of small pebbles, and then to calculate the run lengths of pecking on each colour of food. In the first 100 pecks, the mean run length on red food was found to be 5 for a group of controls, as compared to 20 for a treated group ($P < .005$, 2-tailed Mann-Whitney U-test). And the mean for the number of runs on each stimulus type for the first 100 pecks was 5 for the

cycloheximide-treated group, compared to 13 for the control (.002 < P < .02, 2 tailed MANN-WHITNEY U-test).

A most important aspect of cycloheximide's action is that visual and auditory input must be received by the chick for at least 3 hours immediately after injection on day 2 if there is to be retardation of learning visual and auditory tasks. If auditory input is considerably reduced during this period but visual input remains unaltered, treated chicks will be slow in learning visual tasks, but they will be protected from the drug's action on auditory learning. Chickens which are kept in darkness for 3 hours with normal auditory input are subsequently slow at learning auditory, but not visual tasks. Complete absence of visual input is not essential for protection from the drug's effect on visual learning. Protection also occurs, for example, if the chicken views parallel or other non-intersecting lines presented in the frontal field, and spots or crosses in the peripheral field. Spots or intersecting lines viewed in the frontal field do, however, result in slowed visual learning. The pattern of visual input associated with cycloheximide's effect on visual learning is therefore very specific (ROGERS & DRENNEN, 1978).

No obvious lesion or cell degeneration was observed by light microscopy either one day or 14 days after cycloheximide treatment (ROGERS et al., 1974).

Use of cycloheximide to demonstrate lateralisation

Cycloheximide, 20 μg dissolved in 25 μl of sterile physiological saline, was injected into either the right or the left side of the chicken forebrain on day 2 of post-hatched life. The contralateral side was injected with the vehicle alone, and a control group received saline into both sides. These injections were made symmetrically, the entry point for the needle being approxiamately 2 mm from the midline and equidistant from the rostral and caudal poles of the hemisphere and the tip of the needle 3 mm from the top of the skull. In their second week of life the chickens were tested monocularly on the visual discrimination and habituation tasks, and auditory habituation was tested binaurally.

Three treatment groups of chicks were tested successively for visual discrimination learning, visual habituation, visual detection and auditory habituation. The three groups were: 1) saline in both hemispheres; 2) right side saline, left side cycloheximide; 3) right side cycloheximide, left side saline. There were a total of 48 chicks and therefore 16 in each treatment group. Where monocular testing was possible these were subdivided to give six groups, each containing 8 animals and constituted by having right or left-eye occluded chicks in each of the 3 conditions.

There is a complete decussation of optic nerve fibres in the avian brain. Visual input can be restricted to the right or left tectum by occluding the opposite eye. Each tectum, in turn, sends its major visual projection to the ipsilateral telencephalon.

Visual Discrimination Learning.

Learning rate of the visual discrimination task, as indicated by the number of errors in the last 20 pecks, is presented in Figure 1. When the chicks were tested with their left eyes occluded, learning occurred if the right side of the forebrain was treated with either saline or cycloheximide. But, when the left side had been treated with the drug, no learning occurred. With the right eye occluded, learning occured in control chicks which had been

treated with saline on both sides of the brain, but it did not occur in those that had been treated with the drug in either the right or the left side of the fore-brain.

Thus, the left side of the brain appears to be able to perform visual discrimination learning independently of the right, but the right side cannot do so without the left.

This lateralisation of learning ability is also apparent in the controls which have received bilateral injections of saline; those tested with the right eye occluded learned significantly more slowly than their counterparts tested with the left eye occluded.

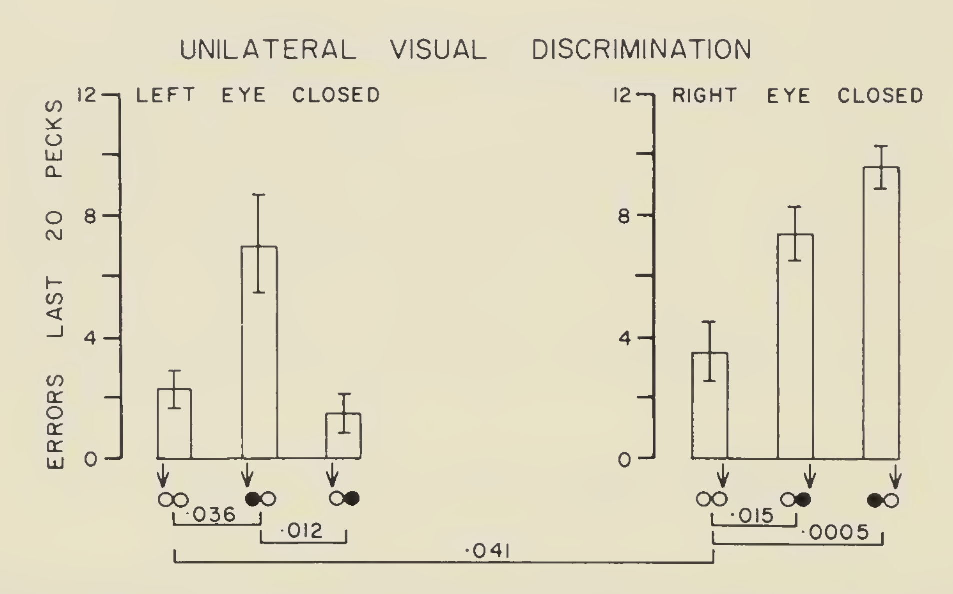


FIGURE 1. Rate of learning on the visual discrimination task is indicated by the number of errors, pecks at pebbles, in the last 20 pecks of testing. Slower learning gives higher values. Means and standard errors are plotted for 6 groups, each containing 8 animals. The pairs of circles underneath represent each side of the fore-brain; an open circle means that that side was injected with saline, and a black circle means that side received cycloheximide. The arrows indicate which side was largely in use during testing, e. g. an arrow to the left side means that the left eye was occluded, and vice versa. MANN-WHITNEY U tests have been applied between each group and every other group. Significant P values are given at the bottom of the figure.

Visual Habituation.

Cycloheximide treatment applied to either the right or left side of the fore-brain had no differential effects on the rate of monocular visual habituation, regardless of the eye used during the test. On the fourth presentation of the novel visual stimulus, the treated groups oriented to it for times no longer than the control group, indicating that visual habituation learning can occur in either hemisphere, or alternatively that it occurs at a site below the forebrain. It should be noted that the visual habituation task uses the lateral, peripheral field of vision; whereas the visual discrimination task uses frontal, binocular vision. This may provide one possible explanation why visual discrimination learning is asymmetrically localized and visual habituation is not.

Those animals in the group treated on the left side and tested either binocularly or with the right eye occluded were found to orient to the novel stimulus on its first presentation for a significantly longer time than any other group. This suggests that the right hemisphere is somewhat more responsive than the left to novelty when the chick first detects it, a finding supported by tests for visual detection.

Visual Detection.

The right side of the brain was somewhat more responsive to small novel stimuli detected in the peripheral field of vision. While the chick was feeding novel objects were simultaneously moved into each peripheral field of vision. Control animals had a somewhat greater tendency to turn towards objects detected by the left eye. (The preference for left eye response over right eye response was 2:1.) This result is suggestive of the right hemisphere being more involved with response to novelty than is the left hemisphere, but further study is necessary.

Auditory Habituation.

Chickens treated with cycloheximide on the right side of the brain habituated to an auditory stimulus (a banging sound) at the same rate as controls; in 9.0 ± 2.0 (mean ± S.E) presentations for the treated group, compared to 9.7 ± 2.1 for controls. But those treated on the left side required significantly more presentations to habituate; 18.0 ± 2.0 presentations, $P < 002$; 2-tailed MANN-WHITNEY U test. Auditory habituation learning must therefore occur more readily in the left side of the fore-brain.

Attentional Persistence.

Attentional persistence was tested binocularly on the task with red and yellow food scattered on a back-ground of small red pebbles. There were three groups of chicks each containing 12 animals; one injected with saline in the left hemisphere and cycloheximide in the right, another with the converse treatment, and a control group treated with saline on both sides. The number of runs of pecking on each stimulus type for the first 100 pecks of the test was scored. The mean run length on red food for the group treated with cycloheximide in the left hemisphere was 51 ± 10 (standard error), and this was significantly above the mean value of 22 ± 7 for the saline control group ($.002 < P < .02$, 2-tailed, MANN-WHITNEY U test).* The mean run length on red food for the group injected with cycloheximide on the right side was 29 ± 9 which did not differ from the score for the control group. Therefore, the group treated with cycloheximide in the left hemisphere is switching between the available stimuli less often than the other two groups. This is the same kind of attentional persistence found previously to occur after bilateral treatment with cycloheximide, and so this action of the drug is localised in the left hemisphere.

Attack and Copulation Behaviour.

The chickens treated in the left side of the fore-brain were noticed to have an increased likelihood of attacking or copulating with the experimenter's hand or the novel visual stimulus. This was studied using standard Hand Thrust Tests for attack and copulation (ANDREW, 1975) which rank attack and copulation scores from 1 to 10. For attack a score of 1 is given for binocular staring at the attack stimulus, a hand moving at beak level, and a maximal score of 10 is given for attack-leaping at the hand with neck arched, hackles up

* The experimental and control values for mean run length on red food reported here are higher than those reported above. This happens because of batch variations. However, since one is working on differences within a given batch, this does not matter.

and pecking. For copulation scoring a horizontal hand is first moved and then held stationary at chest height: a score of 1 is given for walking over the hand and points are added for crouching, treading, pelvic thrusting and circling up to a maximum score of 10. Each test is repeated 3 times and average taken on each day up to an age of 11 days. The results are presented in Figure 2. There were 8 animals in each group. A testosterone-treated group has been added for comparison (25 mg of testosterone oenanthate administered on day 2). The group treated with cycloheximide in the left side of the fore-brain showed a remarkable increase in attack and copulation, comparable to that of the androgen-treated group (e. g. for attack scores on day 11, P = .01 for difference between control and left-side treated groups; and for copulation on day 11, P = .001 for the difference between the same groups; 2 tailed MANN-WHITNEY U-tests). None of the other groups (the control group, the group treated in the right side, or the bilaterally-treated group) showed any increase in attack and copulation. Cycloheximide treatment of the left side must generate some imbalance which releases these behaviours either directly, or, possibly, indirectly via hormonal release. A unilateral disinhibition of sexual and aggressive behaviour has occured.

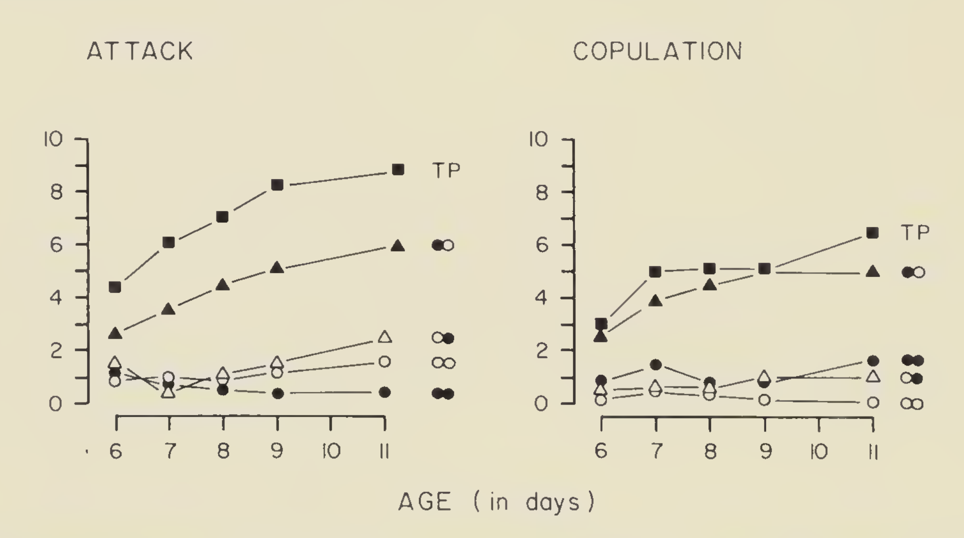


FIGURE 2. Attack and copulation have been scored according to a ranking procedure (ANDREW, 1975; YOUNG & ROGERS, 1978). For either of these, each animal was tested 3 times on a given day, and an average taken. The overall daily mean values for groups of 8 animals are plotted for each treatment. The pairs of circles indicate fore-brains as in Figure 1. The plotted symbol represent: – O, controls injected with saline into each side of the fore-brain; ● cycloheximide in both sides; Δ cycloheximide in the right side, saline in the left; Δ cycloheximide in the left side, saline in the right; ■ TP, 25 mg testosterone oenanthate, Primoteston (Schering).

Conclusions

Visual discrimination learning, auditory habituation learning and aspects of attention switching which are altered by cycloheximide treatment appear to be better represented on the left than on the right side of the chicken fore-brain. The right side is more responsive both in detection of and initial orientation to novel visual stimuli. There is a lateralised control mechanism for suppressing sexual and aggressive behaviour, which is disinhibited by cycloheximide treatment of the left hemisphere. It is therefore postulated that the left hemisphere is concerned with complex integration and learning, and possibly also with the suppression of sexual and attack behaviours, whilst the right hemisphere is more concerned with scanning the environment for novel stimuli. The right side may monitor

the environment and select inputs for the left side, where they can be further processed and stored as memories.

This left-sided localisation of complex neural integration in chickens may represent an evolutionary precedent for left hemisphere dominance for song control in birds such as the Canary. The fact that so many behaviours are lateralised in the chicken brain also raises the possibility that functional lateralisation occurred quite early in evolution.

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SYMPOSIUM ON
STRUCTURE AND FUNCTION OF BIRD SONG

5. VI. 1978

CONVENER: DIETMAR TODT

Functional Aspects of Sequence and Hierarchy in Song Structure

D. Todt and H. Hultsch

Introduction

In spite of the great variety apparent in the song structure of birds, there is a set of principles common to most oscines. Investigating the functional principles of quantitatively described behaviour concern normally is focussed on one of the following categories of aspects:

1) Interindividual aspects (mechanisms of: individual communication, particularly those concerning reproduction and territory; species recognition and isolation; ecological adaptation.) (Lit. summ.: Morton, 1980; Brown & Lemon, 1977; v. Helversen, 1980; Krebs & Hunter, 1980; Todt, 1979b; etc.)

2) Intraindividual aspects (mechanisms of: acquisition, development, determination, control and performance of singing behaviour.) (Lit. summ.: Konishi, 1965; Dobson & Lemon, 1977; Güttinger, 1980; Marler, 1980; Nottebohm, 1980; Thimm, 1980; Todt, 1979a; Wolffgramm, 1978; etc.)

Although there are numerous interesting points mediated by these aspects, this paper examines only the functional relevance of sequence and hierarchy in vocal communication and vocal control. A short outline on analysis of the various song parameters is given beforehand.

Organization of singing behaviour – bases of functional analysis

The study of functional principles requires the preceding investigation of structural principles (Fentress, 1973; Golani, 1973; McFarland, 1976; etc.). The singing behaviour of birds can be described as multichannel time series of behavioural events (Hinde, 1958; Isaac & Marler, 1963; Todt, 1970a; Lemon & Chatfield, 1971; Nelson, 1973; etc.). Proven steps of analysis are:

(1) Introductory analysis of the behavioural patterning. (Each of the sucessively and simultaneously occurring behavioural events can be regarded as a unit for analysis). – (2) Typification and classification of units according to congruent parameter configuration. (Any value which is measured and related to the units under investigation can be regarded as a parameter). – (3) Analysis of the temporal ordering of the units. (Starting time and duration of units and pauses between them; interval length between certain units, frequency distribution of these data). – (4) Analysis of the structural hierarchy of units. (Units may form patterns, which are in turn units of patterns of a higher structural level. This patterning may coincide with positional ordering). – (5) Analysis of the sequential ordering of units. (Transitional relations between units; type and degree of coordination). – (6) Analysis of parameter variations. (Parameters of units, or unit combinations, may change in time either randomly or in correlation to special events or processes). – (7) Further analysis includes analysing those events which occur simultaneously with the

Abt. Verhaltensbiologie, Institut für Allgemeine Zoologie, Freie Universität, Haderslebener Str. 9, D-1000 Berlin 41

behaviour in question. (Data evaluated with multidimensional crossclassified frequency distributions, statistical tests, etc.).

To approach a complete understanding of the behavioural organisation, the results of the particular steps have to be related to each other, and then have to be investigated by further studies (differenciating system-analysis; (TODT, 1973, 1975a; TODT & WOLFFGRAMM, 1975; WOLFFGRAMM, 1975; THIMM, 1977).

Aspects of interindividual functions

The structure of song results from a temporal arrangement of vocal units that occur in sequential order and form patterns on several different hierarchical levels (Fig. 1; TODT, 1970b; DAWKINS, 1976; SHIOVITZ, 1975; etc.). Most of the functions ascribed to bird song are functions of structural units of the song (=strophe) level. For this "key-role", songs (in the sense of "strophes") fit much better than structures of higher (bouts) or lower (elements, notes) levels.

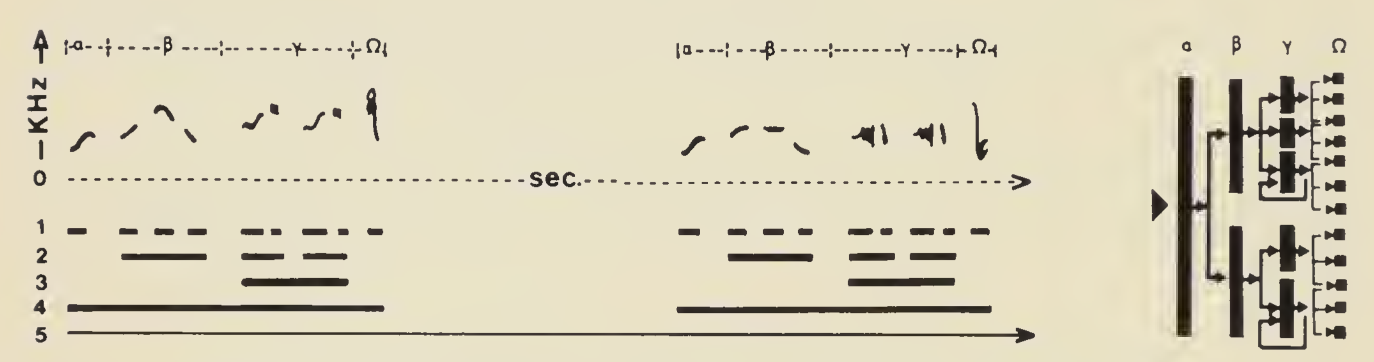


FIGURE 1. Hierarchical organisation of song (schematic). Left: "structural hierarchy"; level 0: sonagraphic patterns; level 1: note (=element); level 2: syllable (here in γ-section); motif (=theme, here in β-section); level 3: series (=tour=phrase); level 4: song (=strophe=train); level 5: bout. Often a "strophe" may be subdivided into α-, β-, γ-, Ω-sections. Right: "Informational hierarchy". Certain element types may occur in certain sections and at special positions within a "strophe". The number of alternative unit types increases from α to Ω. In parallel the frequency of each particular type decreases. Thereby the uncertainty of γ or Ω elements is higher than that of α elements.

1) Songs as units supply many more cues for recognition of species, individual and motivational state of the singer than do elements but, of course, less than do bouts.

2) The messages of songs (typical duration, t. d.: 2–8 sec.) can be perceived and acted upon more quickly than those of bouts (t. d.: 1–10 min and more).

3) The length of silent intervals between songs (t. d.: 2–8 sec.) allows more time for data processing in the receiver than do silent intervals between elements within songs (t. d.: 0.02–0.1 sec.).

4) While duration of pauses between elements within songs are, on the whole, kept constant, the duration of the intervals between songs can be changed (up to more than 100 %) so there is a non-rigidness that allows temporal coordination between vocal signals by communicating birds.

5) The sequential ordering of songs follows a program less fixed than that of the subordinate structures (notes, elements, syllables, etc.) so additionally a qualitative coordination between vocal signals (song types) may occur in communication.

6) The sequence of songs is, however, not at random but depends on an autogenous program operating in the singer. In particular, the "component of throttling-back" and the "component of periodical reoccurrence" of songs can help to avoid monotony in vocal communication, which can be facilitated by equivalent vocal responses in counter singing, for instance (Fig. 5; TODT, 1975a; THIMM, 1980; WOLFFGRAMM, 1978).

Considering the above aspects it would be of basic interest to investigate communication in those species which organize their singing behaviour differently from the type characterised here.

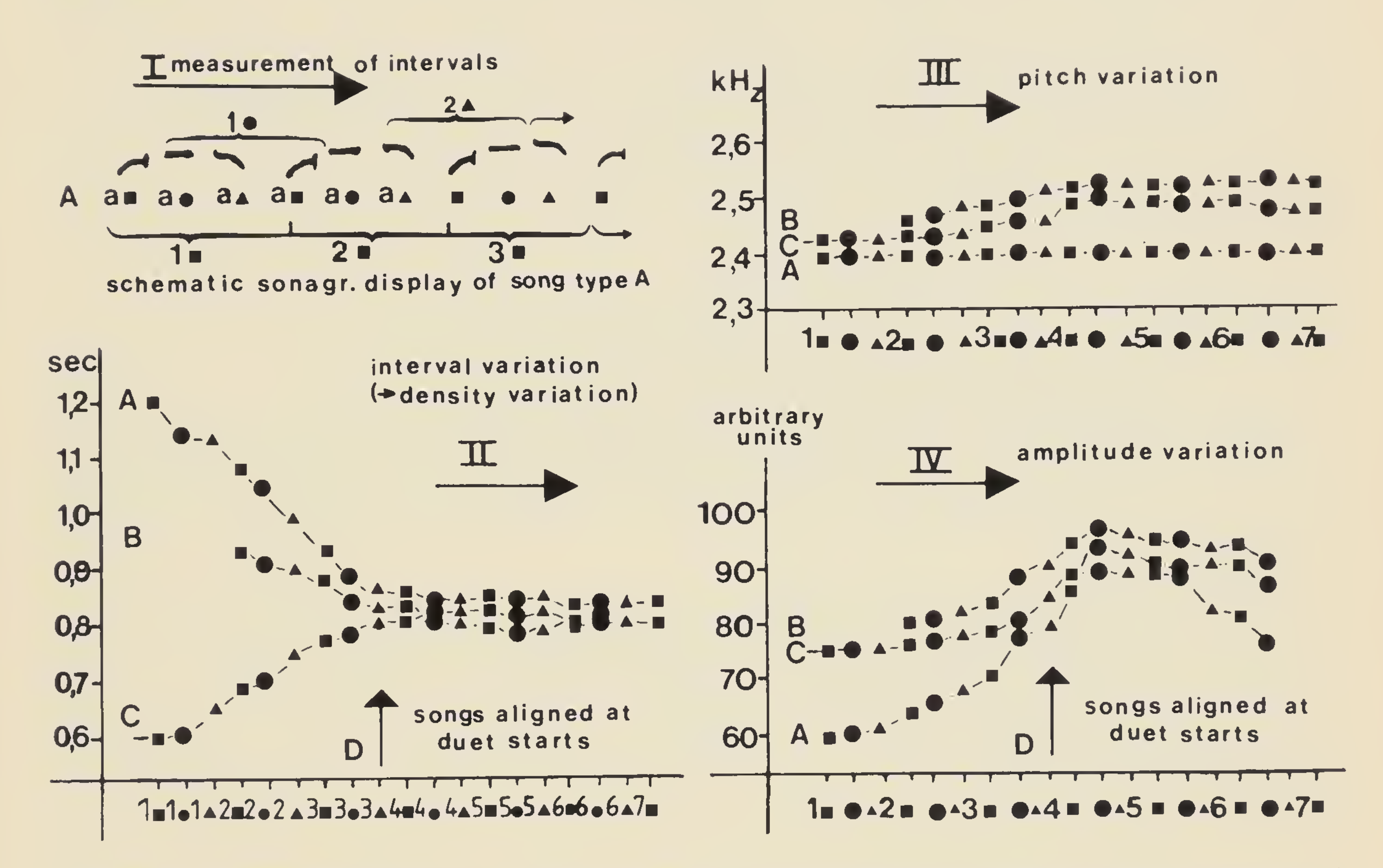


FIGURE 2. Parameter variation in a crescendo song of *Cossypha heuglini*, measured along element and motif sequences (=songs). I: Illustration of measurement. Abscissa of diagram II, III, IV: Running number of unit types or interval. A, B, C: different songs (Fig. 1, L 5). Arrow D: Start of a duet where the ♀ joins in. The crescendo facilitates duetting. Reaching a distinct critical interval between the ♂ motifs triggers the start of the duet. The releasing interval length corresponds to that interval which the ♀ normally sets between the patterns of her duet contribution. Duet was recorded during nest-building period. Coordination type of particular duet contributions may differ according to the particular social function.

In vocal communication, song may facilitate and elicit either vocal or non-vocal reactions. Considering the bioacoustic responses alone one can detect changes in the (autogenous) program of a receiver. Depending on the species, certain specific pattern types and pattern type combinations (including type repetitions) can be changed in the following parameters: (1) amplitude; (2) pitch; (3) vocal density (duration of patterns and pauses); (4) frequency; (5) distance to next reoccurrence; (6) starting time. The particular expression of such changes is again dependent on the individual and on the motivational state of the receiver.

Through and with these changes, communicating birds are able to establish both, temporal and pattern specific relations between their songs (or trains). Preferred temporal

relations results in simultaneous (unisono) or alternating song utterances. Most common pattern-specific relationships result in countersinging or antiphonal duetting. Countersinging occurs between competitive singers, whose vocal repertoires overlap (Todt, 1971). Antiphonal duetting takes place in birds which form stable pair bonds. The duets serve several functions (lit. summ.: v. Helversen, 1980; Thorpe, 1974). The structure of such duets, especially the coordination between the particular duet contributions, can be changed according to their particular social application (Fig. 2; Todt, 1979b).

The most striking characteristic of countersinging is the "matching". Due to it the songs of different singers correspond (more frequently than expected, when random occurrence assumed) to each other in the type of the units actually sung. Characteristics of these correspondences depend on species-specific characters of the "informational hierarchy" of the songs being matched. In the European Blackbird (*Turdus merula),* in which the number of alternative element sequences increases predominantly towards the end of songs, such congruencies can be found almost exclusively in the initial section of songs. On the other hand, in Nightingales *(Luscinia megarhynchos)* the number of alternative element sequences decrease towards the end. Thus response congruencies occur in the middle and terminating section of songs (Todt 1970a, 1971).

There is evidence that a singer, which vocalizes a counter-response (= equivalent response) tries to match a heard prepattern as quickly as possible, immediately after its detection. So, countersinging very often results in a temporal overlapping of equivalent song types.

In territorial neighbours which share vocal repertoires (here: max. song type congruence: about 30 %) sometimes up to 12 % of consecutive songs could be identified as "equivalent" responses. Also we found vocal responses of the "convalent" type. By this means the "vocal follower" may exchange roles, thus becoming the "vocal leader" (presinger; Todt, 1971).

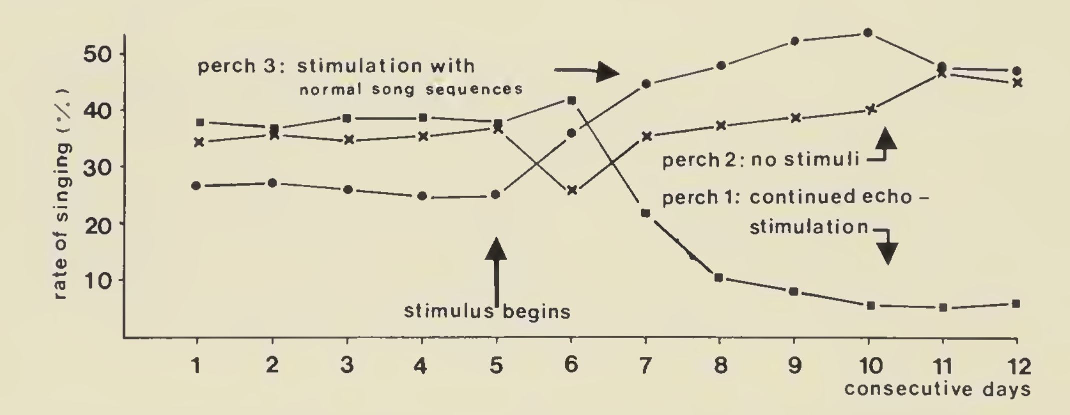


Figure 3. Perch choice affected by auditory stimulation. Perch 1: singing stimulated with song copies placed as "echos" into pauses between songs. Perch 2: No stimulation. Perch 3: Singing stimulated with copies of bouts of the birds own repertoire, without experimental arrangment of artificial echos. (Material: ♂-*Turdus merula)*

We suppose that there are at least two interindividual functions of countersinging. One function is repertoire comparison between neighbouring conspecifics. The other one is establishment and maintenance of a certain distance between the singers. This hypothesis is supported by field studies on European Blackbirds and Nightingales. Results show that in densely settled biotops individuals which share a large part of their repertoires, are

separated from each other by at least 50 m and in general by about 70 to 130 m; on the other hand, individuals with more divergent repertoires may settle and sing between them (Wolffgramm, 1979; Hultsch & Todt, 1979b). This might perhaps be understood from the results of aviary experiments which demonstrate that a bird will avoid singing at a perch, at which it will be continuously confronted by patterns which are equivalent or convalent responses to its own songs (Fig. 3; Todt, 1979b). There is evidence that not only the amount of overlap in repertoires, but also the number of diverse song types uttered, play an important social and ecological role (Kroodsma, 1976; Krebs, 1977; Krebs & Hunter, 1980; etc.).

Countersinging is performed by both territorial individuals and territorial pairs (counter duets). The matching response in a counter duet of two pairs may be triggered and governed by one particular pair member. We suppose that this achievement is reached by learning in and during group singing (Fig. 4; Todt, 1970c).

Aspects of intraindividual functions

In typical communication the interacting systems change their roles (and states) alternatingly. Each of them switches from being sender to being receiver and vice-versa. To understand the intraindividual functions of communication one has to understand the characteristics of both, the two forms of activity, and the manner by which the state changes (Tembrock, 1971).

Data concerning the antiphonal duets of birds are normally evaluated by formal analyses only (v. Helversen, 1980). Experimental analysis is restricted because of the great difficulty in getting adequate responses when one of the partners is replaced, or when its signals are replaced by copies (Todt, 1975b). In contrast, data concerning a counter response can be collected by experimental analysis without difficulty (Lemon, 1968; Falls & Krebs, 1975; Todt, 1979b). In Nightingales and European Blackbirds distinct experimental parameter changes of the acoustic stimuli can predictably raise or diminish the probability for an equivalent vocal response (Fig. 5; Todt, 1970a, 1971, 1974; Thimm, 1980; Wolffgramm & Todt, in preparation; Hultsch, 1979). Here predictions are made based on results from earlier investigations on autogenous song programs (Todt, 1970a, 1970b, 1971).

In many bird species, it makes sense to describe and to analyse the singing by diverse subprograms: for instance, one program which predicts the sequence of songs classified according to initial elements, and another program which predicts the element sequence within a song. Alternative patterns (elements, respectively songs) which are going to be uttered ("pattern choice") are affected by a set of variables (factors, components). Some of them can be traced back to certain specific auditory stimuli (Todt, 1973, 1974, 1975a; Wolffgramm, 1975; Thimm, 1977; etc.).

The decisions which must occur in any variable singing behaviour determine:

1) Which of the alternative units shall be vocalized next?

2) At what time shall it start? When shall it end?

3) In which particular variation shall it be performed?

Certain types of variable singing behaviour, especially the crescendo of Nightingales, robinchats (Fig. 2) and other birds are going to be analysed in testing the "hypothesis of

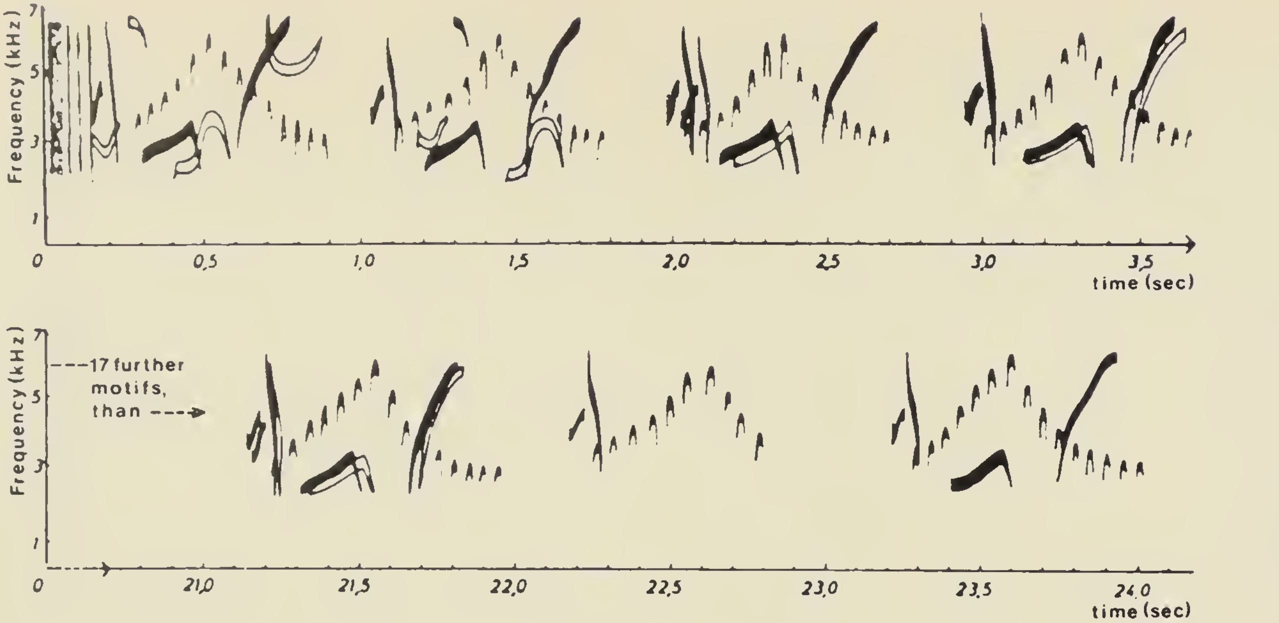


FIGURE 4. Group singing in *Cisticola hunteri*. An antiphonal duet of one pair (black figures) is accompanied by another ♀ (open figures) which matches the patterns of the mated ♀. Notice: between 0–3.5 sec an error in matching is corrected. Dropping of wrong notes starts at motif end; substitution by right notes starts from motif onset.

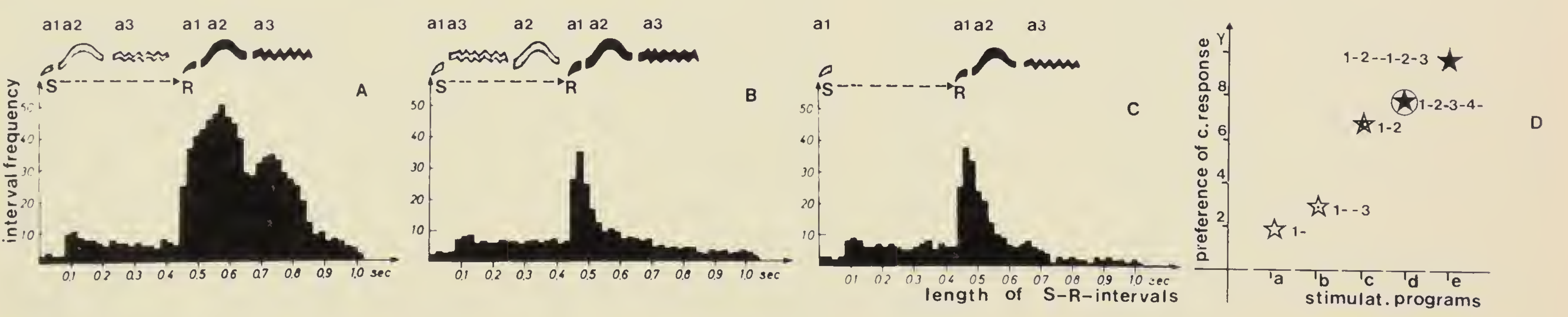


FIGURE 5. Distribution of reaction time intervals of counter responses in Blackbirds. Intervals were measured from start of stimulus pattern (open figures) to start of response pattern (black figures). – A: stimulation with copies of original pattern; B and C: stimulation with copies altered as shown above; D: degree of counterresponse preference at the reaction time interval 0.4–0.9 sec; element sequence of original pattern (1, 2, 3, 4, . . . ; program: d) is altered as illustrated in programs a, b, c, e; program a corresponds to Fig. 5C. Copies which lack the 1st element do not elicit counterresponse.

multiple determination". Questions to be answered include the following. Do these multiple-determinations proceed in discrete steps or in a kind of continuous process? Are these determinations made just before the particular unit is performed or do they proceed earlier? Preliminary results point out that at least one of the determining components underlying the crescendo can only be explained by data processing which spans the intervals separating the particular vocal units (parallel processing, Fig. 2). Further results are strongly desired.

Acknowledgement

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The Role of Periodicities in Avian Vocal Communication

Jochen Wolffgramm

Introduction

Bird song can be examined from two different points of view: (1) its communicative and ecological function concerning the interaction among different individuals (interindividual aspect) and (2) its individual development, its organization and its central nervous control (intraindividual aspect).

The latter aspect includes fluctuations of vocal activity as well as fluctuation of other parameters of vocal utterance. These changes manifest themselves often in rhythmical oscillations, which can be interpreted as effects of endogenous periodicities. Two of these rhythms, the circadian and the circannual periodicity, are well known and broadly studied. The following contribution will be restricted to the subject of infradian short term rhythms, i.e. periodicities the wavelength of which is distinctly shorter than 24 hrs (for references see Todt, 1977). For example, in the singing activity of the Redstart *(Phoenicurus phoenicurus)* periodical oscillations can be found with a period of some hours (Thimm, 1977).

Analysis of periodicities

Further examinations of rhythms according to their effect on song structure and communicative interaction require a quantitative analysis of periodical recurrence. Some procedures have been developed (especially based on autocorrelation functions and power–spectra). These methods however were not totally sufficient for our aims, for neither independence of periodicity nor significances of examined periods of oscillation could be tested statistically – especially concerning rhythms by step (see later). Therefore we developed a new method which qualified for the analysis of periodical recurrence of patterns. The new procedure was called "PUSTA–analysis" ("Perioden–Untersuchung über Sinus–Transformations–Analyse") – cf. Wolffgramm, 1975; Wolffgramm & Thimm, 1976. The basic concept of this analysis is the computation and evaluation of so–called "superposition histograms" which represent the frequency distributions of all the distances that occur between every event to every other event of the same class (Wolffgramm, 1973).

Different components of the control of utterance express themselves in different shapes of the superposition histogram (Fig. 1):

1. In random case there should be linear regression of frequency.

2. Non–periodical influences like sequential components may cause definite deviations from random expectation. The superposition histogram will nevertheless show no recognizable rhythmicity.

3. When there exists an influence from one occurrence of the event to the next one (for instance by a refractory period) we expect that a statistically preferred distance to the next

Physiologisches Institut, Universitätsklinikum Essen, Hufelandstr. 55, D-4300 Essen 1, Bundesrepublik Deutschland.

occurrence will express itself in a peak on the histogram. The next occurrence but one will be less preferred, so that the second peak will be smaller and so on. According to the fact that the deviations from the preferred distance will sum up with increasing order of recurrence, high distant values of frequency will correspond to the random expectation.

4. Periodicities that are independent from the events themselves (superordinate periodicities) are the only influences that lead to periodical oscillations from the beginning of the superposition histogram to its end. The peaks of the histogram represent the distances from one maximum of periodicity to the next one, the next one but one, the next one but two, etc.

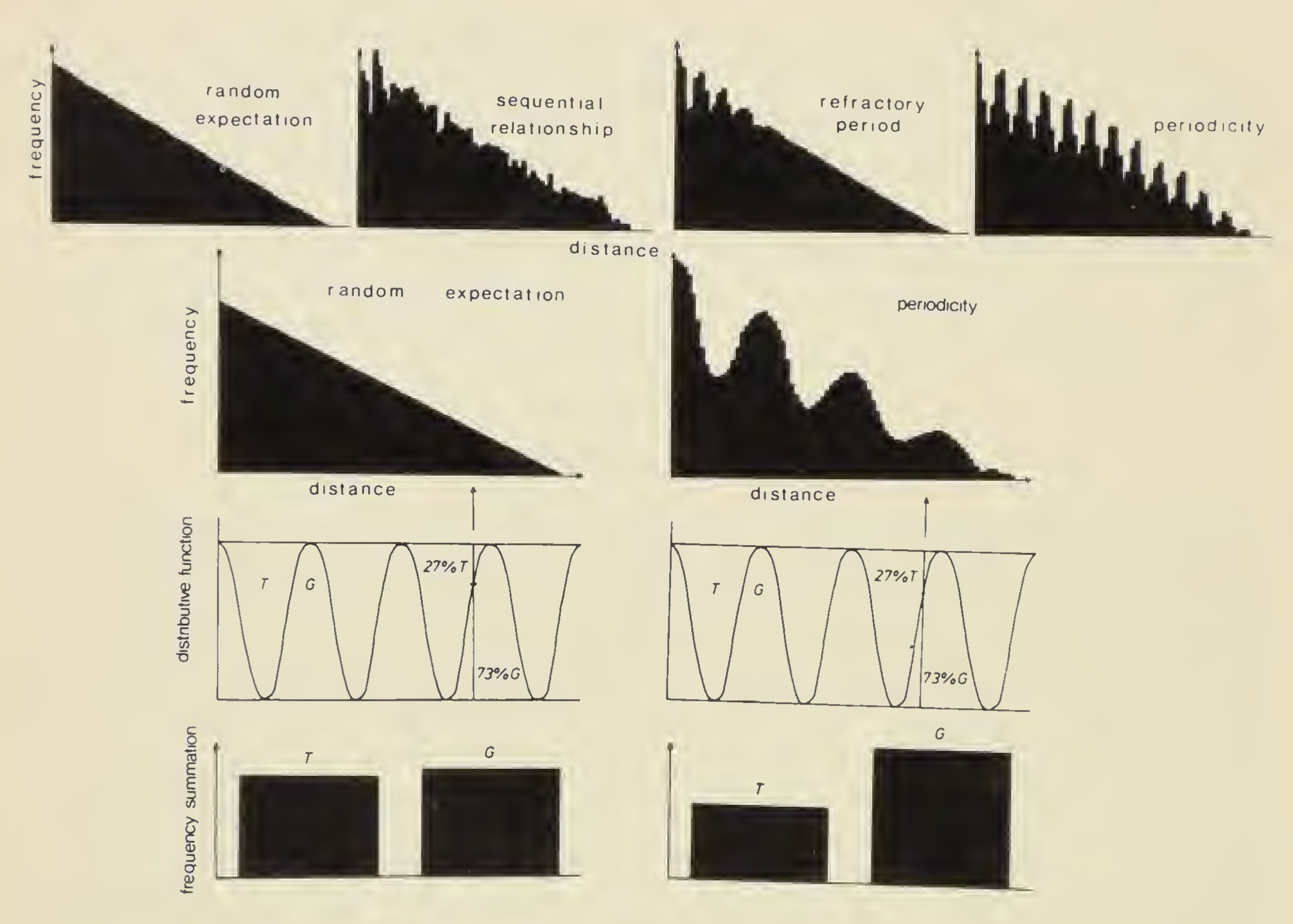


FIGURE 1. Above: characteristic shapes of superposition histograms under different conditions: a.) expected histogram in random case; b.) irregular fluctuations (e.g. in sequentially determined recordings); c.) pseudo-periodical recurrence of patterns (e.g. as a consequence of refractory periods); d.) superordinate periodicity. Below: Principles of PUSTA-analysis. On the right side a random-expected histogram, on the left side the case of periodicity. The plot demonstrates the distributing of frequency values to a G– and a T–portion according to a cosine function. For further explanation see text.

Thus perodical oscillations of frequency within the superposition histogram indicate the existence of a superordinate, independent periodicity. The further aims of analysis are to identify the period of oscillation (or perhaps several different periods that superimpose themselves). This purpose is performed by the second step of analysis (Fig. 1):

Each amount of frequency within the superposition histogram is divided into two portions according to the actual value of a cosine function. Three extreme situations illustrate that procedure:

The whole amount is allocated to the G-portion, when the cosine function has the value of + 1.

The whole amount is allocated to the T-portion, when the value of the cosine function is -1.

G- and T-portion obtain each 50 % of the amount of frequency, when the cosine function has the value of ± 0.

Within PUSTA–analysis the period of the cosine function is varied step by step. If there existed no periodicity, the summation frequencies of the G-portion and the T-portion should be nearly equal. The same result is expected when there exists a periodicity, but the cosine function does not have the same period. In the case however that the period of oscillation corresponds to the period of the cosine function, the summation frequency of the G-portion should be very much higher than that of the T-portion. The relative difference between G- and T-frequencies gives us a quantitative measure for the strength of periodicity. It is quantified by means of the factor of periodicity φ (WOLFFGRAMM, 1975) which is defined by the following formula:

$$\varphi = \frac{G_o - T_o - (G_e - T_e)}{N}$$

G_o: observed summation frequency of the G-portion; T_o: observed summation frequency of the T-portion; G_e: expected summation frequency of the G-portion; T_e: expected summation frequency of the T-portion; N: Sum of all the frequency amounts of the superposition histogram ($N = G_o + T_o = G_e + T_e$). A statistical evaluation of the expected and observed frequencies of G- and T-portions by means of χ^2-analysis has to test the significance of every calculated φ-value. The φ-factors for varying periods of oscillation can be plotted in a diagram (WOFFGRAMM, 1975).

Temporal periodicity

We examined by means of the PUSTA–analysis some species of songbirds. This contribution will refer especially to results concerning Blackbird (*Turdus merula*), Redstart and roller Canary (cf. THIMM, 1973, 1977: TODT, 1968, 1970, 1977: TODT & WOLFFGRAMM, 1975: WOLFFGRAMM, 1973, 1975). We found temporal periodicities with periods of several minutes (Fig. 2). The periods of oscillations varied from day to day. The period of minutes could be superimposed by a period of hours that was mentioned above; it was not connected with the circadian rhythm. In order to examine the influence of periodicity on parameters of bird song we had to confirm the position of the phase of periodicity. This was managed by a computer simulation based upon the knowledge of the period of oscillation. The result of such an analysis is shown in Fig. 3. It was found that the fluctuation of frequency of vocal patterns corresponded well to the course of a sine function. The knowledge of the position of phase made it possible to investigate the influence of the periodicity on the structure of vocalizations. It could be shown that at the maximal range of the periodicity function the duration of vocal patterns was enlarged, whereas the duration of silent intervals was shortened.

Short term periodicities within song guarantee an alternation between periods of vocal activity and periods of vocal inactivity. It is remarkable that in other fields of behaviour

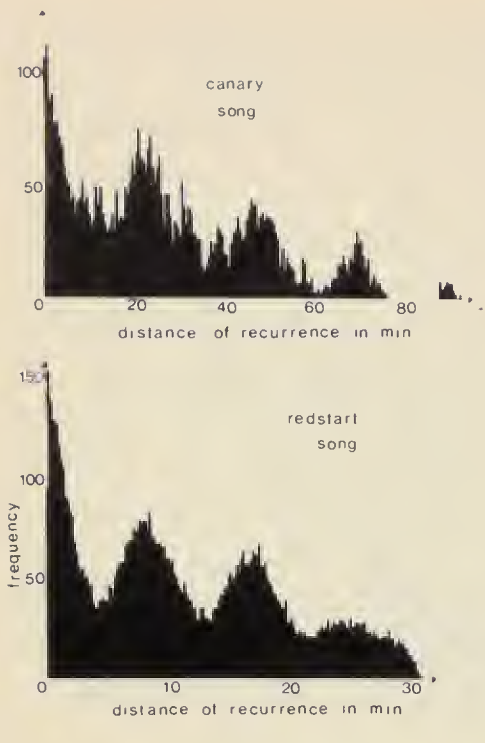


Figure 2. Superposition histograms for the temporal recurrence of vocal patterns in the songs of the roller Canary and the Redstart and of preening in the behaviour of the Mynah-bird (combined from Thimm, 1976; Nguyen-Clausen, 1975; Wolffgramm, 1973).

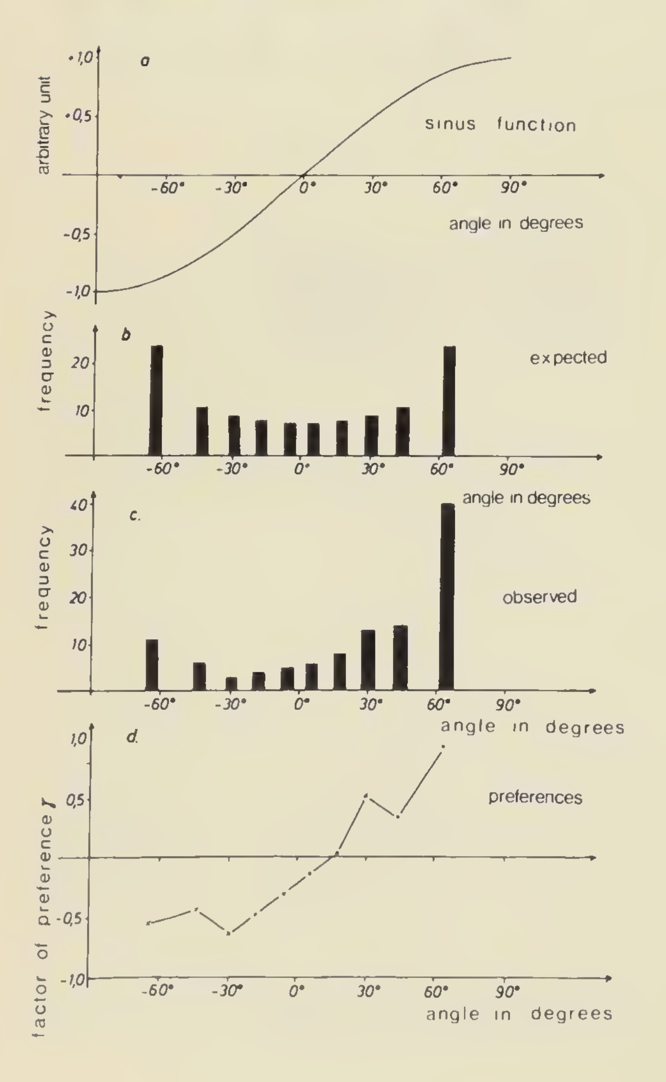


Figure 3. Phase position of temporal periodicity in Redstart song (after Thimm, 1976).

Below the course of the pretended sine function the expected and observed frequencies are plotted.

The diagram at the bottom represents the preferences of occurrence at different phase positions.

also short term periodicities are found (Fig. 2 – cf. Nguyen-Clausen, 1974; Todt, 1977). This suggests a foundamental function of short term periodicities: a variable change among different behavioural utterances is achieved. The rhythms prevent total domination or total suppression of some behavioural acts by others. Thus a variable incorporation of song into the total behavior is achieved.

Periodicities by step

The temporal periodicity of singing described above has no influence on the type of vocal pattern that is to be uttered. The type of pattern however plays an important role in vocal communication. Its choice depends on acoustical stimuli, but is also influenced by endogenous components of control (Todt, 1975; Thimm, 1976; Wolffgramm, 1976). Therefore we examined whether rhythmical influences also had an effect on the decision between alternative types of patterns.

As temporal periodicity had no effect, we had to look at other sorts of rhythms. The evaluations of spontaneous recordings as well as of stimulus-reaction experiments led to the conclusion that there existed a periodicity by step which influenced the choice of pattern. This periodicity did not depend on the temporal distance between two events but only on the number of vocal patterns uttered in the meantime. One step of the period corresponded to the utterance of one pattern. Thus the period of oscillation had to be measured in number of steps (Todt, 1968, 1977). In the three bird species that were submitted to a detailed analysis (Blackbird, Redstart and roller Canary), it could be shown that the level of vocal pattern that was relevant for the counting corresponded to a "strophe" (in German: "Strophe"). Every type of vocal pattern (in Blackbird song: the strophe class, in Redstart song and in Canary Song: the type of tour) had its own periodicity (Thimm, 1977; Todt, 1968, 1970, 1977; Wolffgramm, 1973).

The conclusion that the utterance of a strophe could be regarded as the pacemaker of the periodicity by step was the result of a number of comparative evaluations. Although we cannot exclude the possibility that other species use other vocal patterns it is remarkable that the three species that we examined used the strophe as a step-triggering pattern. In Redstart song it was found that the α-part of a strophe played its part as a pacemaker. Patterns without α-part (that appear rarely) do not have any step–triggering function (Thimm, 1977).

The role of the periodicity by step is in one way similar to those of the temporal periodicity. The latter guarantees variability of singing within the total behaviour; the first one guarantees a variability of the sequence of types of patterns and therefore prevents monotony in countersinging as well as in spontaneous song. In order to examine the relationship between periodicity by step and other components of the control of vocal communication, we investigated the interaction between the component of convalence and step–rhythms. The component of convalence facilitates distinct successions of vocal patterns in spontaneous song as well as distinct responses under stimulus-reaction conditions (Todt, 1970, 1977; Todt & Wolffgramm, 1975). For this purpose periodicity was analysed in definite types of tours which were connected to each other by strong sequential preferences. We found out that in such cases maxima of the periodicity factor occurred at the same wavelength in every type of the succession. This result could be interpreted as a superposition of periodical and sequential influences. The conclusion above

was confirmed by another evaluation. After some types of tours two or more alternative types could be preferred simultaneously. Each of these types possessed its own periodicity. In its maximum of rhythmicity the other type was suppressed. Thus the second type was forced to accept a "secondary" periodicity with the same period, but with a phase difference of half a wavelength. Such an influence was mutual so that the two concurrents were submitted to two nearly identical periodicities.

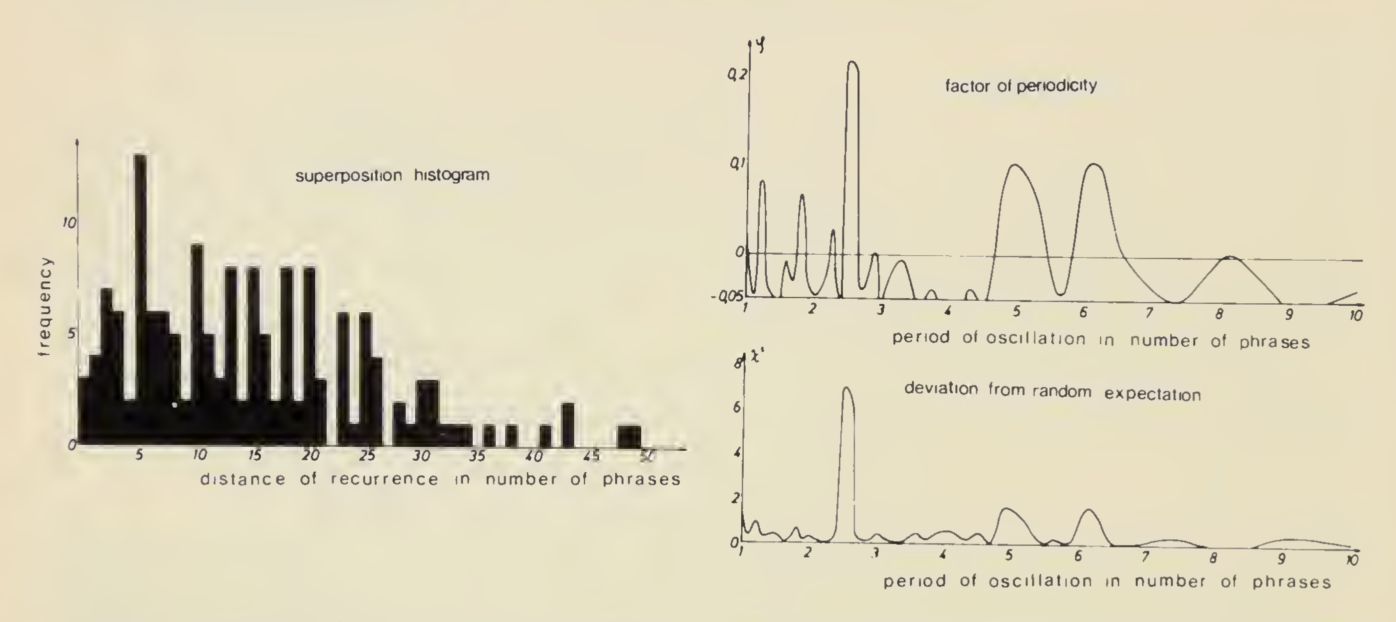


FIGURE 4. Periodicity by step within roller Canary song. Superposition histogram (left) and diagrams of the courses of periodicity-factor and χ-value (right) are shown for one type of four.

The results presented in this contribution should illustrate the function of periodicities by time and by step as endogeneous influences. The first one facilitates singing in concurrence with other forms of behaviour; the latter takes place in the decision between several types of vocal patterns. In both cases, variability is guaranteed when external stimuli are lacking. Under the condition of vocal inputs the temporal periodicity influences the general readiness of response whereas the periodicity by step superimposes the influences of vocal response and thus once more guarantees variability and individuality of song.

Acknowledgement

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The Function of Feedback-Mechanism in Bird Song

Franz Thimm

A bird uttering its territorial song performs a communicative function within this behaviour. Consisting of successive vocal patterns this behaviour is controlled by the central nervous system of the bird. Endogeneous and exogeneous factors influence the accoustical behaviour. The central nervous control of the communicative utterances consists not only of one-way-orders from superordinate to subordinate centers, but also of feed-back mechanisms. The aim of this paper is to review some of these feed-back mechanisms and to discuss their possible functions in the vocal communication. According to von Holst and Mittelstaedt feed-back mechanisms within central nervous control of behaviour can be fundamentally divided into two groups (V. Holst & Mittelstaedt, 1950):

a) Endogeneous feed-back mechanisms occurring in the nervous system can be interpreted as being copies of efferent messages. These copies of efferences can especially cause short term modifications within the control system.

b) Sensory organs record the effects of the behaviour uttered by the organisms. This feed-back returns as reafference into the central nervous processing center. They play an important role in the control of utterance as can be shown by experiments of deafferentation (Konishi, 1965; Nottebohm, 1970).

Reafferent feedback

A singing bird hears its own song. Hereby a vocal reafference takes place, the effects of which on the structure and function of bird song are to be analyzed. One can suppose, but it is not obvious, that a bird reacts vocally not only to vocal patterns of other individuals, but also to feedback patterns of its own song.

Concerning the question of whether or not reafferent feedback causes vocal reactions some remarkable results can be discussed (Thimm, 1977; Todt, 1970 a & b, 1971, 1975; Wolffgramm, 1975):

- Within spontaneous song of some bird species, repetitions of the same class of pattern are statistically preferred. The same species react to a playback of their own song with equivalent responses. Both results seem to be related and can be subsumed under the effect of equivalence (Fig. 1).
- Birds can respond to playback stimuli with definite vocal patterns which are not equivalent to the vocal stimulus. The comparison of spontaneous song and stimulus-reaction experiments show that statistically preferred succession of patterns correspond to stimulus-reaction sequences (effect of convalence).
- Further parallels can be found concerning additional parameters of a bird song, for example, positions of equivalent successions of tours within spontaneous canary song. These successions are preferred particularly at the beginning of the strophe. In

Physiol. Institut der Deutschen Sporthochschule Köln, Carl-Diem-Weg, 5000 Köln 41, Bundesrepublik Deutschland.

corresponding manner equivalent and convalent response in stimulus-reaction experiments occur only in the beginning of a strophe.

These results suggest that vocal reafferences act as a positive feedback and thus cause vocal responses. Equivalent or convalent successions of vocal patterns within spontaneous song can be interpreted as an effect of reafferent self-stimulation (cf. WOLFFGRAMM, 1976).

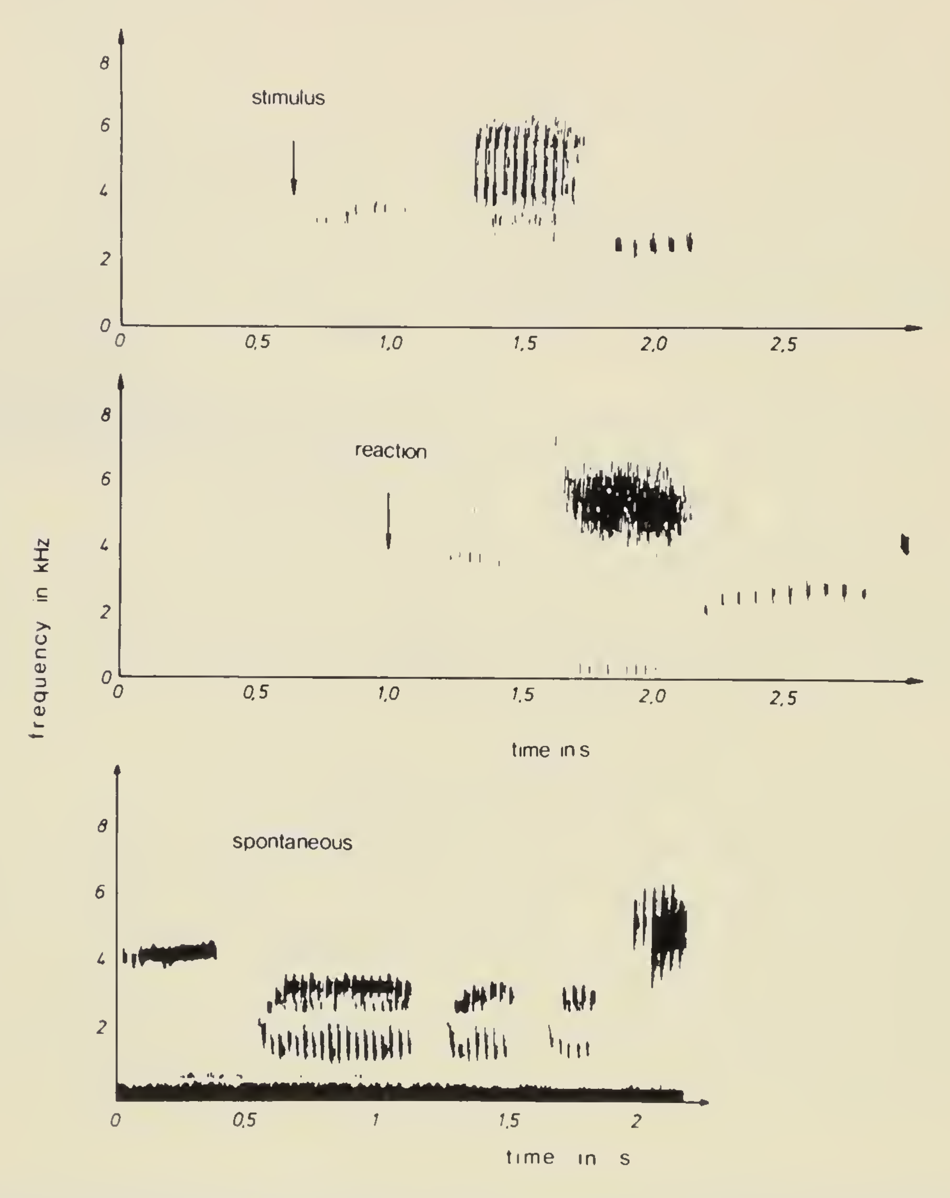


FIGURE 1. Sound spectrograms of equivalent vocal reaction under S-R conditions (above) and equivalent succession of tours (below) in Roller Canary song (slightly modified after WOLFFGRAMM, 1973).

Endogeneous copies of vocal efferences

We also examined the question whether copies of efferences could influence vocal communication. These effects should not correspond to the effect of exafferences (in contrast to the reafferences). Results that referred to such an influence were described independently for several species of song birds (THIMM et al., 1974; TODT, 1971, 1975; WOLFFGRAMM, 1975; cf. LEMON & CHATFIELD, 1971; FALLS & KREBS, 1975). Exemplarily, the effect of this song feed-back can be described as follows.

Within rapid repetitions of one type of pattern the probability for a new succession of the same type decreases step by step (TODT, 1975; WOLFFGRAMM, 1975, 1976). In birds

with definite strophe periodicity (for instance the Blackbird, *Turdus merula)* another effect to inhibitional feed-back can be seen:

When maxima of periodicity were formed by more than one strophe of the same class, the first maximum was reduced and the next occurrence of a strophe of that class could be found with raised frequency at the second maximum of periodicity (TODT, 1970b, 1975). We called the concerned influence of control: component of throttling back.

The effects of this copy of efference depend only on the strophes which were uttered by the bird itself and cannot be caused by external stimuli. Throttling back can be described as an inhibitory feed-back. Its effects can be seen especially in respect to two regards:

1) The specific inhibition of equivalent succession is particularly strong, when the intervals between the vocal patterns are short. It decreases with increasing duration of the interval (Fig. 2; THIMM, 1973, 1976, 1977; THIMM et al., 1974; WOLFFGRAMM, 1974, 1976; cf. DOBSON & LEMON, 1975).
2) At a high level of inhibition, that is caused by the component of throttling back, the duration of vocal patterns is short. Their duration is positively correlated with the temporal distance to the last occurrence of the same type (WOLFFGRAMM, 1975).

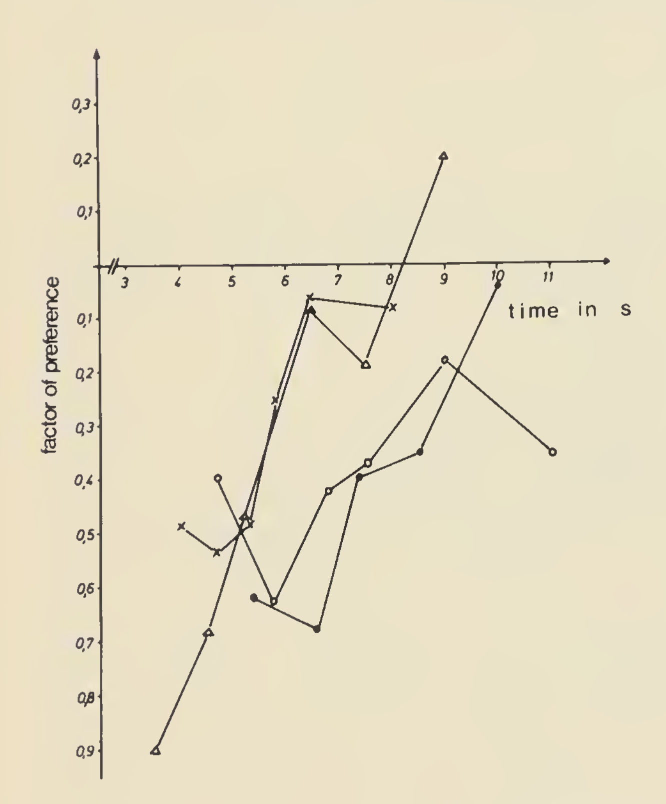


FIGURE 2. Factor of preference for succession of equivalent strophes (strophes of the same class) in spontaneous Redstart song depending on the interval between the two subsequent strophes.

Negative feed-back and communication

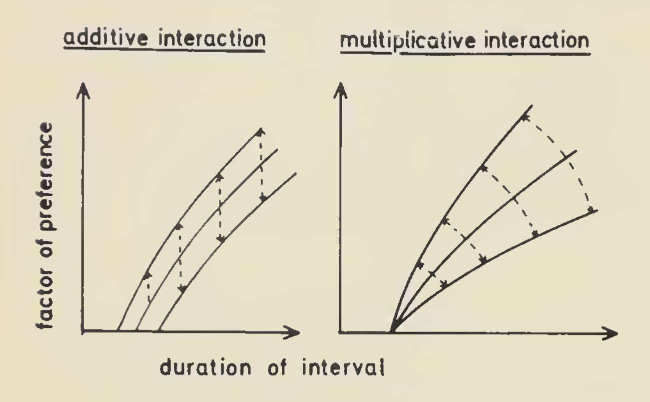
The influences of equivalence and convalence, as well as the influence of throttling back, have a large effect upon the sequence of vocal patterns. It can be supposed that vocal communication is also influenced. We analyzed the interaction between the components of vocal response and the component of throttling back in the song of the Redstart *(Phoenicurus phoenicurus)*. One important effect of throttling back is to inhibit equivalent succession of strophes. The inhibition decreases with time. Therefore both the component of equivalence and the component of throttling back counteract. In these experiments successions of equivalent strophes were analyzed under three different conditions of afference:

1) No stimulus between two subsequently sung strophes,

2) Equivalent stimulus between two subsequently sung strophes,

3) Nonequivalent stimulus between two subsequently sung strophes.

The experiments were not separated into three distinct series, but were integrated into one experiment containing all the conditions of afferents in statistical sequence. This procedure guaranteed an optimal comparability between the different results.



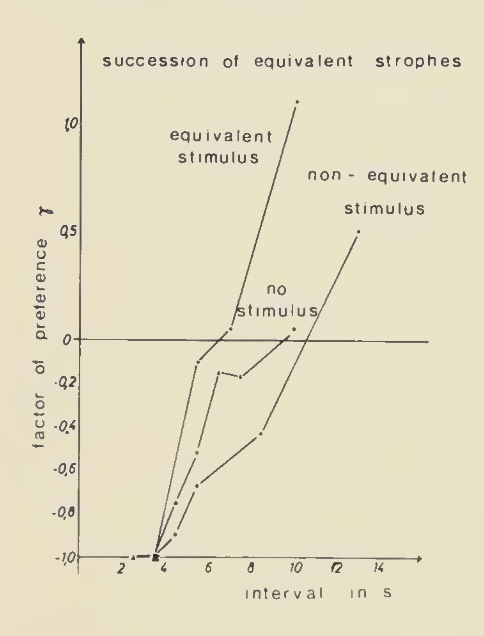


FIGURE 3. Below: Factors of preference for the succession of equivalent strophes in Redstart song depending on the interval between the subsequent strophes. The plot demonstrates three different conditions of afferents: no stimulus between the strophes, equivalent stimulus or nonequivalent stimulus within the inter-strophe-interval. – Above: Theoretical relationship under additive and multiplicative interaction between vocal input and throttling back.

These experiments led to the following results: the lessening of inhibition was accelerated by an equivalent external stimulus and slowed down by a nonequivalent stimulus (Fig. 3; TODT, 1975; THIMM, 1976, 1977). From this and other results we can deduce the following principles affecting control. The different decrease of inhibition slope can be interpreted as an interaction between equivalent response and endogeneous throttling back:

– When a stimulus is lacking, the reafference works as the only vocal input and leads to a light positive response.

– When the stimulus is equivalent, reafference and exafference act in the same direction. The increased influence of equivalence interacts with the throttling back (which is not dependent on afferences).

– When the stimulus is nonequivalent, reafferences and exafferences contract each other so that the influence of equivalence is reduced in relation to spontaneous song.

Hence, the 3 stimulus situations represent different degrees of influence of equivalences. Assuming an addition as the mode of interaction between throttling back and equivalence,

we would expect a shifting of the curve of preferences by a constant amount either upwards or downwards. However, this is not the case. Instead we find a different decrease of inhibition slope than we would expect in the case of a multiplicative interaction.

The conclusion from these series of experiments is that the mode of interaction between equivalence and throttling back must be a multiplicative one. Other experiments carried out on the Redstart, as well as on the Blackbird and Canary, suggested corresponding conclusions. Other additional components of control were included. In all 3 species it was found that the influence of throttling back was multiplied with the sum of the influences of equivalence, of convalence and discrete periodicities. The result of this computation represents the facilitation for one type of vocal pattern. Diagrams of the interaction of the control components postulated for the 3 species are published (Todt, 1975; Todt & Wolffgramm, 1975; Thimm, 1977; Wolffgramm, 1975).

A comparison of the results obtained by different authors shows that the influences of throttling back in song behaviour seem to be widespread. This fact indicates that throttling back has an essential importance for song structure and consequently also for song communication. Working as a negative feedback throttling back prevents permanent positive feedback, by acoustical reafference and so leads to an uninterrupted response to its own song and therefore to a totally stereotyped-printing. Uniform external acoustical stimuli would also degrade the bird to a machine of response.

Concerning Blackbird song this hypothesis could be confirmed by computer simulation of different concepts of control interaction (Todt & Wolffgramm, 1975). This throttling back in cooperation with other, e. g. periodic influences, guarantees the variability of song utterance.

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Structure and Function of Antiphonal Duets

Dagmar von Helversen

Duetting – a vocal ritual performed either simultaneously or alternatively by the partners of a pair – is a characteristic vocalization in many species of birds. Despite occasional transitions, duetting should be differentiated from both simple, reciprocal contact-calling and from soft, partner-directed tones of "intimacy" and "tenderness".

As with all considerations of function in biology (Bock & v. Wahlert 1965), the question about the function of duetting has two aspects: (1) what is the ecological function, the biological role of duetting and (2) how does such a complex coordination in the behaviour of two animals work, how is such a system constructed?

The ecological role

The fact that duetting has repeatedly evolved independently in phylogenetically separate lines indicates that a strong selective pressure is active. Duetting is obviously part of a uniform syndrome which includes monogamy, very often monomorphy of the sexes and a pantropical distribution (e.g. in East Africa approximately 10–15% of all bird species perform duets (Payne 1971), whilst in temperate zones duetters are the exception: for lists of duetting species see Thorpe 1972 and Kunkel 1974). Almost all explanations for the biological significance of duetting which have been put forward so far are not mutually exclusive but rather are capable of being simultaneously applicable. One should therefore expect that, despite the syndrome character of this phenomenon, various functions receive different emphasis in different species. In the following, a compilation of the most important hypotheses for the ecological significance of duetting is presented, followed by a brief analysis.

(1) Acoustical contact in dense vegetation (Thorpe 1963, 1972)*
(2) Ritualized appeasement of aggression between the partners (Kunkel 1974)
(3) Transfer of information (in the sense of messages) (Seibt & Wickler 1977)
(4) Isolation mechanism (Diamond & Terborgh 1968, Wickler & Uhrig 1969)
(5) Protection from predation (Harcus 1977)
(6) Recognition of sex (by means of vocal sexual dimorphism) (Hooker & Hooker 1969)
(7) Synchronization of reproductive behaviour (Dilger 1953)
(8) Strengthening of the pair bond (Armstrong 1963)
(9) Territorial display (Diamond & Terborgh 1968, Seibt & Wickler 1977)

For all these interpretations it is just not possible to exclude that duetting – at least for the one or the other species – possesses one or more of the proposed functions, even if only

* I have tried to cite the authors stating the particular hypotheses especially accentuated. Further detailed discussions can be found in Immelmann 1961, Payne & Skinner 1970, Todt 1970, Payne 1971, Wickler 1976, etc.

Zoological Institute, University of Freiburg, Bundesrepublik Deutschland.

to a minor extent. But which function is likely to be the general, primary driving selective force of selection in the evolution of duetting? At this point we can exclude hypothesis (1), since most duet-singers live in biotopes characterized by good visibility or since the partners fly together before they start duetting (Payne & Skinner (1970), Kunkel (1974). Furthermore, Wickler's (1976) considerations seem to me to be the decisive objection to all explanations except (9): duets are much too loud to be of significance solely to the mate. This type of communication could be achieved adequately by quiet, less obvious behaviour, which does, in fact, occur. There is probably a considerable selective pressure against unnecessary loudness (because of hazards due to increased pressure from enemies (Marler 1955) and the squandering of energy). On the other hand, it is also obvious that a territorial pair can best demarcate its territory together: since mated males defend their territories more decisively than unmated males and also more effectively since the partner can help in a critical situation, they should let a potential rival know as soon as possible that they are mated. The simplest way of doing this is to perform the territorial song in the form of a duet. – It is thus obvious that territoriality combined with permanent monogamy (which are especially prevalent in tropical areas and which spare conspicuous sexual dimorphism, thus resulting in the syndrome mentioned) does indeed provide a starting point to develop duetting.

Possibly then duetting was a precondition for one or the other function mentioned above, which secondarily may have become significant. For instance, defending the territory together could simultaneously serve to strengthen the bond between the partners (in a fashion similar to the "pseudo-attacks" of grey geese (Lorenz 1935)). Additionally, the pair-bond is also maintained by the high degree of mutual coordination and habituation which is elaborated during a long process by partners who are initially strange to one another (Thorpe & North 1965). The striking universal specificity of male- and female-repertoires, which is maintained even by those duet-singers having the richest and most complex duets, should be advantageous in quickly recognizing the sex of a conspecific.

The structure of duets

Duetting occurs in a variety of structural complexity, ranging from simple calls repeated more or less precisely to highly elaborate duets consisting of a rich repertoire of elements, which the partners develop into pair-specific motives. This series of progressively increasing complexity is definitely not an evolutionary improvement, but rather it demonstrates that duetting has evolved repeatedly and independently from different evolutionary stages of bird song. The following examples (chosen more or less arbitrarily) serve to illustrate different grades of complexity:

(a) In the simplest case, the male and the female each can make use of only one species-(or population-) specific call or motive. In the duets of many barbets, for instance, these calls are repeated many times with more or less exact timing (Payne & Skinner 1970). A section from the stereotyped duet of *Trachyphonus d'arnaudi* is given in Fig. 1a.

(b) A second example is provided by the duet of the White-browed Robin Chat, *Cossypha heuglini* (Fig. 1b). In this species, the male has at its disposal a considerable number of different motives whose sequence approximately corresponds to the solo song of thrushes (Todt 1970a; Todt & Hultsch 1980). The female's contribution to the duet

is, in essence, just one shrill, sharp scream, whose frequency is somewhat higher than that of the male motives. The female can adjust the rhythm of its call to fit the male-part (Thorpe 1972, Wickler 1974).

(c) The third stage is represented by those duet-singers which have large repertoires of elements available to both partners. This multiplicity of elements gives rise to a new dimension of complexity: the fashion in which these elements are combined in the duet.

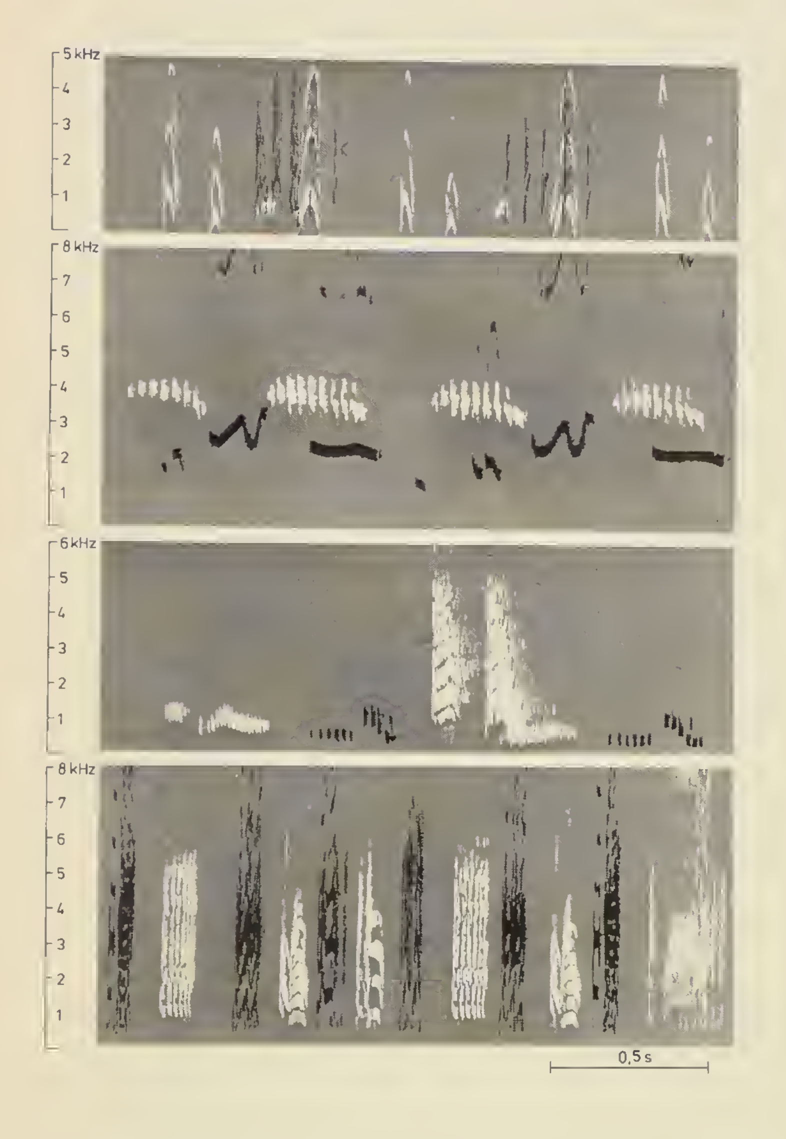


Figure 1. Excerpts from duets of four duetting species; the part of one partner is shown in white, that of the other in black.
a) *Trachyphonus d'arnaudi usambiro*
b) *Cossypha heuglini* (courtesy of D. Todt)
c) *Laniarius funebris* (courtesy of W. Wickler)
d) *Dicrurus adsimilis*

In the case of *Laniarius funebris* (Fig. 1c) a pair has several distinct motives characterized by the type and combination of two to three elements. Whereas neighbouring pairs have most of their elements in common, the combination of elements is in many cases pair-specific, as Wickler (1972) could demonstrate by comparing the amount of overlap of elements and duet-motives among three neighbouring pairs of these shrikes. This result is shown in Fig. 2: Particular combinations of elements occur in the duets of only one of the three pairs (and very regularly in this pair). They do not appear in the duets of the other pairs although they use the same element-types, but in different combinations.

Whereas in *L. funebris* usually two to four elements form a motive which is repeated over and over again, the duet of the African Drongo, *Dicrurus adsimilis*, is a very complex series of many different elements given alternatively by male and fermale (Fig. 1d). The repertoire of a pair may comprise more than 70 elements between which complicated sequential relationships exist.

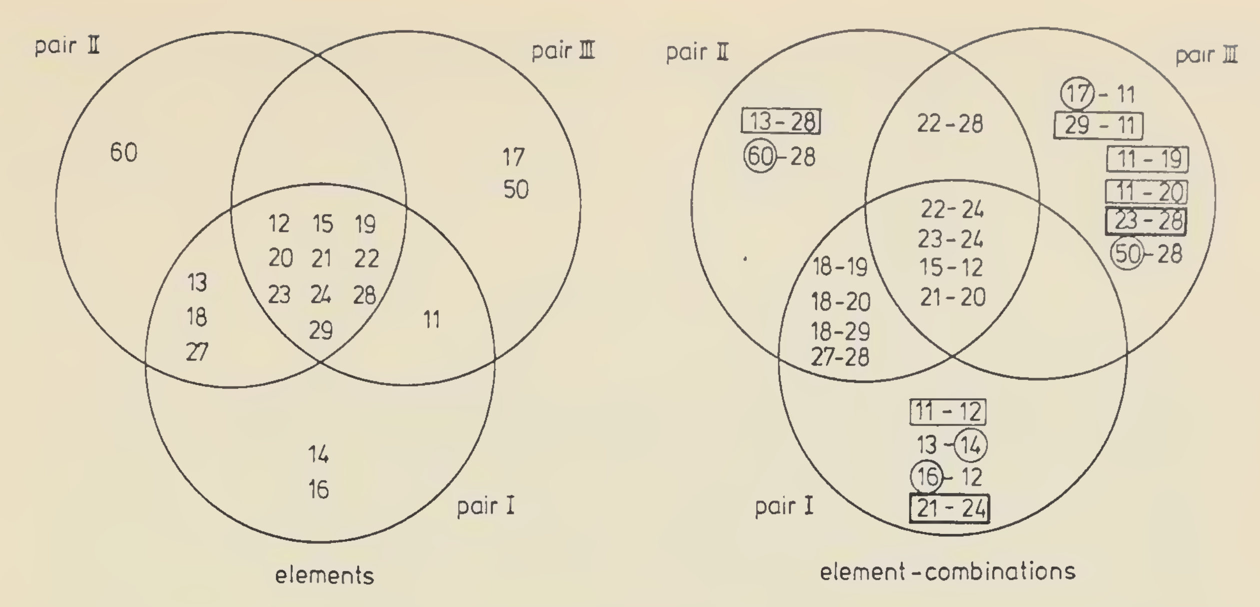


Figure 2. Elements (a) and element-combinations (b) in the duets of three neighbouring pairs of *Laniarius funebris*. Each circle comprises the elements (or element-combinations) used by one pair. ○ combinations which are pair-specific because of the use of an individuum-specific element; □ pair-specific combinations of elements available to two pairs; □ pair-specific combinations of elements common to all three pairs (from Wickler 1972, modified).

Information transfer in the duet

If, in a duet, one bird by presenting its own elements changes the probability of appearance of elements in its partner's song (because the partner answers him), then there has been a transfer of information between the partners. This does not mean that this information has a concrete meaning, i. e. that it is a message for the recipient; the transfer of information is only a pre-condition for the transfer of messages.

An analysis of the matrices containing transition frequencies of elements of both partners in a duet – for all cases studied so far – has revealed a highly significant deviation from a random sequence. This nonrandom distribution may not be due solely to mutual responding but may be also due to the bird's endogenous program ("Eigenprogramm"), i. e. the sequence of elements which is intrinsically preferred by each singer. The extent of these simultaneously present influences may be different in both birds (v. Helversen & Wickler 1971).

The following examples demonstrate these two components. The effect of answering is particularly evident in the duets of *Laniarius funebris,* studied by Wickler (1972). The highly significant nonrandomness already present in the succession of the first two elements of a duet can only be explained by a specific reaction of the partner to the introductory element of his mate. The influence of the endogenous program in these shrikes is mainly limited to the preferred repetition of the same element, as Wickler was able to show using long series of calls from a single singing bird.

In the duets of the White-crested Jay Thrush *(Garrulax leucolophus)* endogenous program and response-tendencies superimpose much more obviously. The duet of this species consists of a relatively short phrase (approximately 3–4 s, consisting of 20–30 elements); the course of the phrase is almost entirely preset. Since for the various elements the probability of occurrence changes during the duet, the duet was termed a "non stationary process" by Soucek & Vencl (1975) (cf. Wickler 1976). But, in terms of the two influences discussed, this could mean that only the endogenous component is

responsible for the preset progression of the duet, whereas the reply-component may be entirely stationary: at any position in the duet a bird may use the same element for an answer to a certain element of the partner. This seems to be true for the male element M24, which has a "switching function" and moves the duet forwards or backwards to "phase III" (Vencl & Soucek 1976).

In the Drongo, too, both components determine the occurrence of a specific element. Whether a certain element is more endogenously programmed or whether it is more likely to be an answer to a partner's element can be checked by using triplet combinations. For instance, in the transition matrix A_i B_k A_j (Fig. 3) element A28 often occurs after the combination A28-B23. Is A28 linked more to the singer's own preceding element or to the partner's B23? If element A28 is linked to the own preceding element one should expect that the probability of occurrence is independent from the partner's element in between. The expected values can be calculated for the sequences A28-B23-A28 and A28-B_k-A28 and can be compared to the values in the matrix. The χ-test reveals that the hypothesis "A28 linked exclusively to the own previous element" is not true (P = 0.0005) i. e. element B23 has an influence on the partner's element.

	A_{24}	A_{26}	A_{27}	A_{28}	Σ
$A_{24}B_{23}$					
$A_{24}B_R$		5	1		6
$A_{26}B_{23}$	1		6	3	10
$A_{26}B_R$	1		37		38
$A_{27}B_{23}$	1			4	5
$A_{27}B_R$	3			35	38
$A_{28}B_{23}$	1	1	1	9	12
$A_{28}B_R$	2	24	8	1	35
Σ	9	30	53	52	144

Figure 3. Transition matrix A_i B_k A_j. The element-pairs A_i B_k are followed by the elements A_j with the given frequencies. In B_R all elements used by bird B, except B23, are summarized.

One can recognize the fluctuation between "leading" and "responding" particularly well if one observes the way in which one bird "proposes" a new group of elements (v. Helversen & Wickler 1971). During a continuously recorded series of duets, the Drongos changed over to new elements, one could say to a new theme, in the 11th duet. The way in which this happened is very instructive. Up to the 11th duet bird A had sung only the elements A10, A16, A18, and A26; bird B had employed a repertoire containing 7 elements. The 11th duet starts with two elements B20 and B21 to which bird A does not reply. (Twice previously these two elements had not been answered, thus causing the end of the duets). The third call from B introduces a new element, B6. Bird A replies to B6 with element A30 which had likewise not yet been used – and from this moment on, bird A has switched into a completely different part of its repertoire. It doesn't sing any of the elements used in the preceding 10 duets but uses only the three elements A30, A76 and A25 instead. Bird B introduces, in addition to B6, four new elements, thereby forsaking virtually all of the elements which had been sung previously. Obviously only element B6 provided the necessary associations for the "proposed" theme, whereas B20 and B21 didn't give an adequate entrance.

This example shows how one element can suffice to cause the partner to switch to a new part of his repertoire. It also demonstrates how attentively each partner takes note of what his mate sings, since it can react, i. e. "answer" within a few tenths of a second. Maybe we should think of responding as "switching" in general, as tuning into a particular portion of the repertoire, whereby each element is connected by a multiplicity of associations to its own neighbouring elements and to those of the partner.

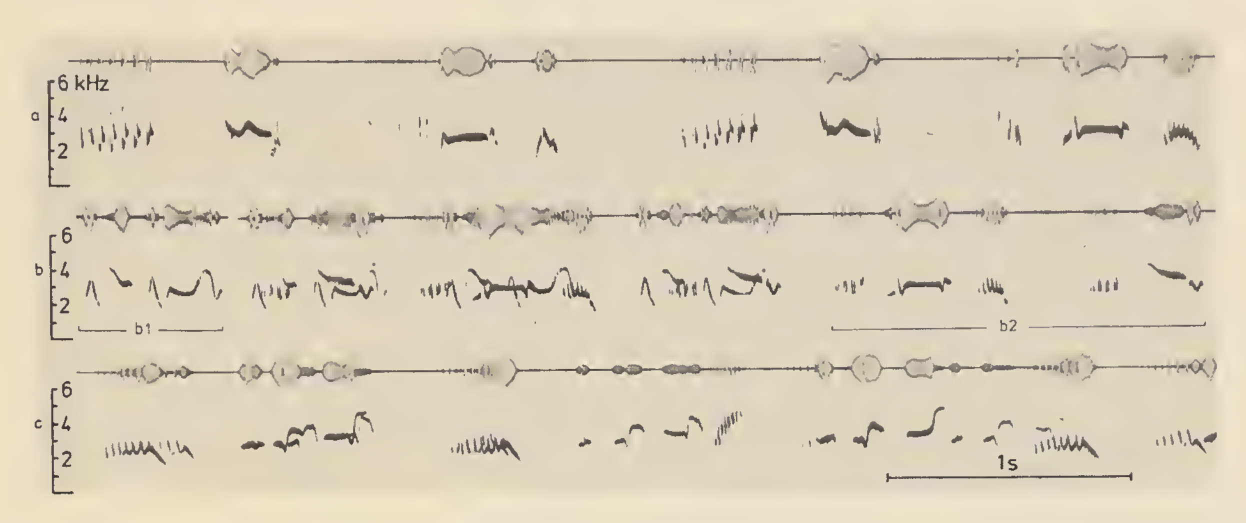


Figure 4. Excerpts from solo-song (a), duet-song (b) and counter-song (c) of the Anteater Chat *Myrmecocichla aethiops.* b_1, b_2: motives which are repeated by each partner in the course of the duet. During the counter-song, males tend to sing identical motives. – Lower trace: continuous recording using a real-time spectrum analyzer whose output modulated the intensity of an oscilloscope-beam. Upper trace: simultaneous recording of the amplitude modulation. (I gratefully acknowledge H.-U. Schnitzler's kind help and advice with these recordings).

Perspectives

Up until now, virtually only descriptive investigations and only few experimental analyses of duet-singing have been undertaken. The questions concerning the ecological significance (territorial function, pair-bonding) are, in essence, suited to an experimental approach (cf. Todt 1975, Harcus 1977, Wiley & Wiley 1977). Beyond this, investigations in the following areas have been started: 1) the ontogeny of duetting (Thorpe 1972, Anzenberger 1974, Tyroller 1974); how does a particular pair practise and improve its duets? How does the complete sexual specificity of the repertoires come into being? 2) The relationships of duetting to chorus-singing have been studied. What is the ecological significance of chorus-singing performed by many tropical species of birds? Preliminary observations indicate that the Anteater Chat *Myrmecocichla aethiops* could be a particularly good subject for the study of these questions. These chats, which live in social groups, demonstrate within one species different types of songs: The males perform a typical turdid solo song which is only given before dawn (Fig. 4 a). Countersinging is very typical at this time; two or even three males sitting about 50 m apart tend to sing identical motives (Fig. 4 c). As dawn breaks, the group flies together and starts duetting (Fig. 4 b). In addition, from time to time, the group congegates at different locations, and, as if in response to a command, at once begins a loud chorus-song. Presently one can only guess about the function of the different types of song. It probably is concerned with the stabilization of the group, pair-bonding within the group, and territorial demarcation of the group as a whole.

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Structure and Function in Great Tit Song

J. R. Krebs and M. L. Hunter

Introduction

The song of the male Great Tit (*Parus major*) consists of a simple repeated phrase of (usually) between two and six notes. The song is repeated in short bursts of variable length, and each male has a repertoire of song types, so that a series of bursts of one song type is usually followed by a switch to another song (Gompertz, 1961; Krebs, 1976). In southern England, repertoire size normally varies between one and six songs. Males in this region start to sing in late December or early January when spring territories are first defended, but after most birds have paired, and song continues through the breeding season until the young hatch out in late May. The most active singing period is usually in March and April (Hinde, 1952) and most song is produced in the early morning (Hinde, 1952; Hunter, 1978). In Great Tits, song is primarily a male vocalisation, but females sing occasionallv, for example when the mate is away from the territory; we will not, however, discuss female song.

Our aim in this paper is to describe some experiments and observations designed to investigate the following questions: (i) Does song play a role in territorial defence? (ii) Are song repertoires important in territorial defence, mate attraction, or kin recognition? (iii) How does the acoustic environment influence the structure of Great Tit song? We only have space to review the results in brief, and more detailed accounts are published elsewhere or are in preparation.

Song and territorial defence

As we have mentioned, male Great Tits sing most during the territorial season, which suggests that song may play a role in maintenance of territories. This is commonly assumed to be a function of male song in birds, but there is little direct evidence for the idea.

We tested the hypothesis that song is a territorial signal by removing pairs from their territories in mixed deciduous forest in the spring, and occupying the empty territories with a system of loudspeakers broadcasting song (Krebs, 1977a; Krebs et al. 1978). Previous experiments had shown that empty territories in deciduous forest are soon reoccupied by new pairs or unmated males, some of which came from suboptimal habitat (farmland) surrounding the study area. This led us to predict that empty territories "occupied" by loudspeakers would be invaded more slowly than control territories with no sound or with a control sound.

The experiments were all done in a 6 ha copse of mixed deciduous forest near Oxford, England. In each experiment, we plotted the territories of all the pairs (which were colour ringed) in the copse and recorded their songs. The broadcasting system for "occupying" a territory with song or control sound consisted of a Uher 4000 IC tape recorder equipped with an endless loop cassette (c. 8 mins at 19 cm per sec.) linked through a 15 watt amplifier to four loudspeakers. Each loudspeaker was at the end of a 50 m cable in a

Edward Grey Institute, University of Oxford, Oxford, Gr. Britain

different part of the occupied territory. During an experiment, the playback system was arranged to operate for 8 minutes every hour from dawn to dusk (in the "repertoire experiments" referred to later the tape played for 8 minutes every half hour for three hours after dawn to simulate the early moring song peak). During the 8-minute cycle each of the four loudspeakers was activated in turn for 2 minutes.

The experimental procedure was to remove all the resident pairs on one morning (as nearly synchronously as possible), and continuously observe the pattern of reoccupation of the control and experimental territories. The control territories are either silent or occupied by a loudspeaker system playing a control sound on the schedule described above.

The results of two experiments of this design involving a total of six experimental and ten control territories were essentially similar: the first birds to invade the wood always settled in the control areas (irrespective of their position in the copse), and only after these areas were filled did birds eventually occupy the experimental territories. The control territories were usually occupied within a day, and the experimental areas were fully occupied only after two or three days. Our conclusion is that broadcast song is an effective "keep out" signal in the short term. It is not surprising that our loudspeakers failed to keep out invaders for a longer time, as real birds normally respond with song or chasing when an intruder enters a territory. The eventual invaders of our experimental territories normally started their occupation after tentative singing near the edge of the experimental area.

Song repertoires: Territory defence, sexual selection or kin recognition?

Territory defence:

If song acts as a territorial keep out signal, why does each male have a repertoire of song types? One possibility is that repertoires are important in territory maintenance. For example because the different songs could be used in different contexts (e. g. LEIN 1973, LEMON, 1968; TODT, 1970; TODT & HULTSCH, 1979) or because the repertoire of songs might have the effect of deceiving intruders into avoiding an area by simulating the sound of several occupants (KREBS, 1977a, b). We tested whether or not a varied repertoire of songs enhances the effectiveness of song as a keep out signal by means of loudspeaker occupation experiments of the design described earlier. In this case we compared controls, and two types of song occupation: single songs and repertoires. We did three experiments involving a total of eleven experimental and seven control territories. In all three experiments, the sequence of invasion of empty territories was: control, single song, repertoire. Further, the difference in time to occupation of the single song and repertoire areas seemed to be greater when the repertoire contained more songs. This experiment shows that song repertoires increase the effectiveness of song as a keep out signal, although it is not yet possible to say exactly why.

Sexual selection and kin recognition

Two other hypotheses which might explain why Great Tits have song repertoires are that repertoires are favoured by sexual selection (e. g. KROODSMA, 1976; 1977) and that repertoires facilitate kin recognition (TRIESMAN, 1978).

Although male Great Tits normally pair before they sing most intensively in the spring, when a female is experimentally removed, the amount of song produced by a male increases by up to 20-fold (KREBS and COWIE unpub.). Experimentally produced bachelor males usually obtain a new mate within a few hours after which their song rate again declines. Thus it seems likely that song can be important in mate attraction in some circumstances. Following FISHER (1958) one could predict that if females prefer males with larger song repertoires, these males should be mated to females which are more successful at breeding. We analysed two correlates of breeding success, laying date and clutch size; there was no evidence for the predicted effects (KREBS et al., 1978), which indicates that repertoires are not favoured by sexual selection.

TRIESMAN (1978) suggested that learned song repertoires might be a mechanism for kin recognition, the presumed advantage of which is to avoid inbreeding or allow kin-selected altruism between territorial males. Although it is known that many species of birds learn their songs, there is virtually no evidence in favour of the idea that birds learn song from their fathers (KROODSMA, 1974). We tested this possibility in the Great Tit by examining the song repertoires of males known through ringing records to be sons or fathers. The analysis involved categorising all the songs in a population (Marley Wood, near Oxford) into about twenty different types, and any conclusions we draw rely on this classification.

The analysis consisted of calculating the mean number of songs shared between all birds both within and between years, and then comparing the mean number shared between fathers and sons with the mean for the rest of the possible pair combinations. The results showed that there is more song sharing between birds in the same breeding season than between years. Sons do not share more songs with their fathers than do unrelated birds between successive years. There is also no clear trend for songs shared between sons and fathers to be more similar than average for shared songs. We conclude that learned repertoires are unlikely to provide a mechanism for kin recognition between male Great Tits.

There is, however, weak evidence suggesting that female Great Tits avoid mating with males which share songs with the female's father. This is bases on a small sample size, but if confirmed in a more extensive analysis it might show that females use songs as a means of avoiding mating with their fathers. It is not clear, however, why this should favour the evolution of song repertoires.

In summary, there is evidence that song repertoires are important in territory maintenance, but not in sexual selection or kin recognition.

Geographical variation and the significance of song structure

In this section we describe how the structure of Great Tit song is related to the acoustic environment. The effectiveness of song as a long distance territorial signal depends on its transmission through the environment, so we hypothesised that individuals living in different habitats might show adaptations to the local acoustic climate. Our approach was to compare the songs of Great Tits living in two very different habitat types, by recording songs in each habitat type in different parts of the Great Tit's range. We predicted that if song structure is influenced by habitat, populations living in the same sort of habitat but in different places should have similar songs, and that there should be consistent differences

between songs from the two habitat types. MORTON (1975) and CHAPPUIS (1971) showed that species of birds living in tropical forest have lower pitched, purer songs than those in more open country and they suggested that this difference could be related to the greater attenuation of high pitched sounds in forests. We tested this hypothesis for intraspecific variations of Great Tit song.

TABLE 1. Characteristics of songs of woodland and forest birds measured from narrow band sonograms, made with a Kay 6061 B sonagram using the FL2 and linear setting.

	N	max. freq.	freq. range	no. of notes
woodlands				
Spain	111	6461	3098	4.0
Iran	121	6451	3063	3.1
Greece	94	6476	2888	3.0
Oxfordshire	54	6501	3326	3.0
mean woodlands		6467	3067	3.3
forests				
Sweden	67	5563	1798	2.3
Norway	30	5748	2307	2.8
New Forest	36	5491	2118	2.4
Poland	102	5806	2272	2.7
mean forests		5681	2118	2.5

We recorded songs of Great Tits in four places where the birds live in dense forest (Southern England: 51° N, 2° W; Sweden: 59° N, 16° E; Norway: 61° N, 11° E, and Poland 53° N, 24° E) and four places where they live in open woodland or parkland habitats (Spain: 35° N, 6° E; Iran: 30° N, 52° E; Greece 39° N, 23° E; Oxfordshire 52° N, 1° E). We also measured, for each habitat type, several variables which could influence transmission of songs: (a) Acoustic attenuation of sounds of different frequencies; we broadcast and rerecorded a tape at sites in Spain and Poland. The tape contained 26 sounds, including artificial tones and modulated notes covering the range from 2.0 to 7.5 Khz, and a selection of Great Tit songs. Broadcasting and recording were done with Stellavox SP7 tape recorders, a Sennheiser MKH 415 T microphone, a polyplanar loudspeaker, and a Nagra DH amplifier. The tests were done at a height of 5 m on days with no wind during the first two hours after dawn. Attenuation at 40 m was analysed using a Plurimat S signal analysis computer which computed a power versus frequency spectrum for the whole tape. (b) Vegetation density: we calculated tree canopy volume from plot samples. (c) Territory size: we estimated the distance between singing males. (d) Avian song community: we estimated the number of species singing frequently in each study area, as an index of potential 'sound competition'. We only counted species whose song overlaps in frequency range with that of Great Tits. (e) Other data: we also noted the meteorological characteristics (from standard records) and body size of the birds at each study area (from SNOW 1953).

The most important differences between woodland and forest songs are shown in Table 1. Forest birds sing songs of lower maximum frequency, narrower frequency range, and

fewer notes than those of woodland birds. It is remarkable that these features are more similar between woodland sites separated by many hundreds of kilometres than between forests and woodlands much closer together. Woodland songs clearly converge on one general pattern and forest songs on another.

Two of the habitat variables we measured also showed a particularly striking contrast between woodland and forests. The density of foliage was much higher and the territory size much larger in forests than in woodlands. Although there were more species singing in forest, the total amount of song as estimated by dawn counts in Spain, Greece and Poland did not differ significantly between the two habitat types. The acoustic attenuation tests also revealed a potentially important difference between woodland and forest. In the latter habitat, sounds above about 5.6 Khz are more strongly attenuated, while below 5.6 Khz there is little difference between habitats. This coincides well with an observation that forest Great Tits tend to avoid high frequency sounds: woodland Great Tits sing twice as much as forest birds in the range 5.6–8.00 Khz.

Our results suggest that some of the differences between forest and woodland songs can be accounted for by greater attenuation of high frequencies in forests. The larger territories of forest birds probably also place a premium on avoiding high frequencies, which attenuate rapidly with distance. If forest songs are better designed than those of woodland birds for long distance transmission, there must be some counter selection pressure in more open habitats favouring the woodland song type. We suggest that this is unlikely to be that high frequencies are easier to produce, but perhaps the wider frequency range and greater complexity of woodland songs is of advantage in mate attraction or territory maintenance.

Acknowledgements

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SYMPOSIUM ON NEUROANATOMY AND NEUROPHYSIOLOGY OF THE AUDITORY SYSTEM

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Response Characteristics of Auditory Neurons in the Cochlear Ganglion of the Starling

Geoffrey A. Manley

This paper describes data obtained from microelectrode recordings from the eighth nerve of the Starling, in co-operative work with Dr. H.-J. Leppelsack of the Ruhr University, Bochum, Federal Republic of Germany. A new surgical approach was used, actually an adaptation of the intra-cochlear recording technique already used successfully in mammals and lizards (e.g. Manley, 1977; Robertson & Manley, 1974; Weiss et al., 1976). In the barbiturate-anaesthetized bird, the middle ear was opened laterally and a hole made in the bone overlying the *recessus scala tympani*. Through this hole, the cochlear ganglion was visible and accessible to electrode penetrations. When the head was held firmly, this method allowed stable recordings, on occasion to more than one hour. Such recording times often permitted us to collect a great deal of information from individual neurons. The technique also allowed the preselection of the best frequency of the neurons encountered, according to their location in the cochlea. Stimuli were delivered free-field in a sound-isolated anechoic chamber. Glass micropipettes provided excellent signal-to-noise ratios and presumably recorded from Nodes of Ranvier near the cell bodies of the ganglion. Data are reported from 333 units in 51 animals.

Both regular and irregular spontaneous activity was encountered (Manley & Leppelsack, 1977). All regularly-firing units were encountered in the apical area of the ganglion and did not respond to pure tone stimuli (at least up to 80—90 dB SPL in the frequency range 50 Hz to 10 kHz). Some neurons in this area discharged irregularly but were also unresponsive to pure tones and noise. Similar patterns of spontaneous activity and responsiveness to sound have been described for the eighth nerve of the cat (Walsh et al., 1972). Neurons unresponsive to sound were presumed to be innervating the lagena macula and were not further studied. This would mean, of course, that the lagena macula has no auditory function. Non-acoustic units had spontaneous rates between 5.6 and 167 spikes/s.

All units sensitive to acoustic stimuli showed irregular spontaneous activity, with rates from 4.9 to 149 spikes/s and an average of 43 spikes/s. This average rate is higher than that reported for the cat (30/s) but lower than for the pigeon (90/s) (Sachs et al., 1974). In time interval histograms, the dead times and modal values are shorter than those described for the guinea pig (Manley & Robertson, 1976), and the decay function is faster than exponential. At this point, it should be noted that no electrical stimuli were used to detect units, neither were swept-frequency search stimuli used. Thus units with zero spontaneous discharge which did not respond to our acoustic search stimuli might have been overlooked, and possible pure-tone insensitive units (Gross & Anderson, 1976) classified as non-acoustic.

Spontaneous data was analyzed from 79 neurons, 22 with characteristic frequency (CF) at or below 800 Hz. Fifteen of these 22 showed preferred intervals in the time

Department of Biology, McGill University, Montreal, Canada

interval histograms, which in most cases corresponded to the CF period (or multiples of it) although no stimuli were present. That this is not a highly sensitive response to low-level background noise is shown by the fact that the average threshold was 53 dB SPL for these neurons. These intervals, which have also been observed in data obtained in low frequency primary fibers of the Tokay gecko (Eatock, Manley & Pawson, in preparation) may be a manifestation of a frequency selectivity built into the hair cell/neuron complex.

Frequency-intensity tuning curves were obtained for 128 neurons using an audio-visual criterion for a just noticeable increase in discharge for threshold. CF's were between 200 Hz and 5.4 kHz, although because midrange neurons are more accessible, the range is probably wider. High CF's were encountered in the basal region of the cochlea, low CF's apically. This frequency distribution is as in mammals, and could be predicted from Békésy's mechanical measurements in the chicken cochlea (Békésy, 1960: 504—506). Similarly, the lack of any special asymmetry in the tuning curve shape (such as the asymmetry seen in mammals at all CF's) could be expected from these basilar membrane resonance curves. Below 800 Hz, almost all tuning curves were sharper on the low frequency side, but above 800 Hz about 60 % were sharper on the high frequency side. At this stage it is not clear to what extent the middle ear affects this distribution. Although units near 1 kHz were the most sensitive (down to 9 dB SPL) their Q_{10dB} sharpness coefficients were unexpectedly low (Manley & Leppelsack, 1977, Fig. 6), due mainly to a tendency for the low frequency slope to be low. It is interesting to note in this connection that Konishi (1969) found an exceptionally good time-locked response of bird cochlear nucleus units to rapidly repeated clicks. The broadness of the filter properties of most of these units may be involved with the requirements for high time resolution. Many of the components of bird song are extremely short and rapidly repeated. This question requires further investigation. The total range of Q_{10dB} values was 0.8 to 9.6, as in the pigeon (Sachs et al., 1974). It is, however, not easy to directly compare the tuning curves with those of Sachs et al., since the threshold criteria were different and, according to their data, the tuning curve shape alters as iso-rate contours are plotted for different rates. In our data, the best thresholds agree very well with those obtained in the Starling cochlear nucleus (Konishi, 1969). Discharge rates in response to pure tones were very high (average maximum near 300 spikes/s) with instantaneous rates during the initial dynamic phase of the response of near 500 spikes/s.

In 56 neurons, responses to species-specific vocalizations were studied. The stimulus consisted of a 1.5 minute length of tape containing 109 different vocalization components—social calls and portions of the song. This tape had previously been used by Leppelsack & Vogt (1976) in studying the selectivity of neurons of field L of the Starling forebrain to species-specific vocalizations. The stimulus tape was played at different sound pressures in 10 dB steps from 70 dB (peak) down to 30 dB. Responses were tape recorded, photographed later from the oscilloscope and compared to the oscillogram and sonogram of the individual vocalizations. These stimuli were analyzed on a contour-forming sonagraph, so that a fairly accurate idea could be obtained of the frequency-intensity content of each. In comparing these sonagrams with the pure-tone tuning curve, the presence or absence of a response from the cell could, in almost every case, be predicted from the tuning curve and spectral energy content of the vocaliza-

tion. That is, the cells behaved like simple filters. A typical case, to illustrate the analysis technique, is illustrated in Fig. 1. In only two cells and a total of 5 vocalizations did a response clearly fail to appear (less than 1 % of all events). This failure is probably attributable to a form of two-tone or multiple-tone suppression. Given the average shape and sharpness of a tuning curve and the relatively broad-band nature of many of the vocalizations, it was not unexpected to find that cells on average responded to somewhat less than half the vocalizations (range 22—68 %) at 70 dB peak. This defines to some extent the input to the auditory brain centers and forms, as it were, a neural baseline to which the responses of higher centers can be compared. Thus, in field L of the Starling forebrain, neurons respond on average to 15 % of species-specific vocalizations (at 70 dB) with, however, a range of 1 to 100 % (Leppelsack & Vogt, 1976).

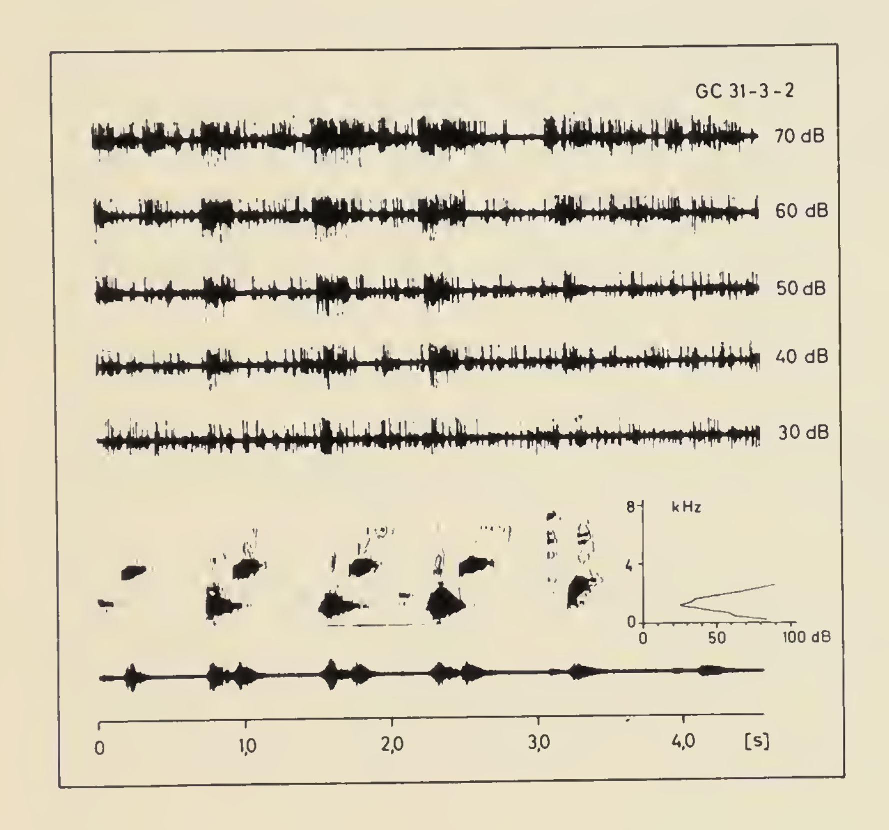


Figure 1. Response of a single neuron to a few species-specific vocalizations. Upper five rows: neuron discharge in response to the same set of sounds played at five different intensities. Below: a contour sonagram of the four main components in this set. The darkness of the contour indicates the intensity in the original song. On the right is the cell's tuning curve plotted on the same axis as the frequency axis of the sonagram. At the bottom is an oscillogram of the vocalizations and a time scale. It can be seen that only low frequency portions of the song evoke a response from the cell.

In summary, in the cochlear ganglion the vocalization responses can be predicted from the tuning curve with very high accuracy and the response selectivity is low. In field L of the forebrain the predictability is low and the selectivity high. It remains to be demonstrated where in the brain this neural processing occurs.

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Experiential Afferent Influences and Development in the Avian N. Magnocellularis and N. Laminaris

Edwin W. Rubel

Three lines of research have led to increasing interest in the avian auditory system. First, a large body of knowledge on bird vocalization has generated interest in relating behavioral capacities to structure and function of the auditory pathways. Second, the unique phylogenetic position of Aves as a second offshoot of reptilian lines promises to reveal valuable insights regarding the origins of the mammalian auditory system (Boord, 1969; Mehler, 1974). Finally, the avian auditory system is currently used in several laboratories as an advantageous system in which to investigate the role of experience in nervous system and behavioral ontogeny (Gottlieb, 1976; Rubel, 1978). Other contributions in this volume discuss avian phylogeny and the relationships between bird song and auditory physiology. In this paper we will consider the qualities of the avian auditory system which lend themselves to study of experiential roles in nervous system ontogeny. In so doing, we will briefly review our own investigations of brain stem auditory nuclei development in the chick.

Statement of the problem

There can be little contention with the statement that the early experience of an organism can influence its behavioral and physiological development. Although some behaviors, and perhaps some species, appear more resistant to fluctuations in the environment, either qualitative (e.g., imprinting) or quantitative (e.g., song recognition) influences of early experience have been discovered for most behaviors thoroughly investigated (Newton & Levine, 1968). Uncovering the neural mechanisms responsible for experiential modulation of behavior development has been difficult, however. While examples of morphological, biochemical, and physiological changes in the nervous system of animals reared in restricted environments are abundant (Gottlieb, 1978), the causative chain of events relating nervous system development to experiential factors is far from understood. At least one reason for this lack of mechanistic information is that there has been little attempt to operationally define, in terms that can be applied to neurons and neural systems, what is meant by "experiential modifications." For example, it is now well known that monocular deprivation of form vision will lead to dramatic changes in the distribution of ocular dominance of neurons in the cat and monkey visual cortex. However, we do not know how that manipulation of the organism's interaction with the external environment alters the cellular milieu of visual system neurons. In other words, while it is known that monocular form deprivation leads to distinct changes in the distribution of light impinging on the retinal surface, how this is translated into chronic changes in the environment of the neurons in the cerebral cortex remains unknown. Stated more generally, in order to unterstand the mechanisms underlying experiential modulation of neural development it is necessary

Co-authors: Thomas N. Parks, Daniel I. Smith and Hunter Jackson.
Department of Otolaryngology, University of Virginia Medical Center, Charlottesville, Virginia, U.S.A.

to define the difference between the "normal" and the "altered" environment of the neurons under investigation. Some chronic or tonic change in the environment of the brain regions that are influenced by early experience must underlie these phenomena.

Viewed in this way, the problem of understanding how alterations in early experience influence neural ontogeny is subsumed under the general problem of tissue interactions in the developing nervous system. Specifically, during ontogeny, as a result of receptor development and synaptic formation along neuronal networks, the neuronal environment becomes subject to both phasic and tonic changes in the external environment of the organism. Modifications of "normal" experience must have differential influence on the ontogeny of neuron structure and function by producing some change, qualitative or quantitative in the afferent input to the neurons under investigation. Thus, integral to understanding the mechanisms by which the early experience of an organism influences neural development is documenting the effects of manipulating the integrity and the activity of afferents on the developmental history of a neural network.

Qualities of a model system

Given the complexity of the nervous system, the task of defining the ways in which afferent input influences the ontogeny of structure and function appears formidable. One strategy for approaching such problems has been the careful selection of a preparation which possesses characteristics particularly advantageous for analysis of the particular topic. When the characteristics of a "model system" have been clearly defined, one can survey a variety of preparations and choose the one which most closely approximates an "ideal" preparation.

A "model system" for the analysis of environmental influences on neural development should possess the following qualities:

1. Genetic homogeneity. Given that there is an interaction of genetic and environmental factors in virtually all developmental events, it is highly desirable to use animals of similar genetic constitution.
2. Homogeneity of the embryonic environment. It is also well known that variations in factors such as circulating maternal hormones, temperature, etc., can have both quantitative and qualitative influences on neural and behavioral ontogeny which may differentially interact with experimentally-induced modifications of afferent input.
3. Simple structural and functional organization. Ideally, it is desirable to have only one or two inputs to a small set of neurons, each of which could be structurally and functionally defined and each of which could be quantitatively manipulated along a continuum from no afferent input to supranormal afferent input. In addition, the neuronal pool should be sufficiently limited and well defined that both structural and functional identification of any subset in possible throughout development.
4. Access to the preparation throughout development. It should be possible to manipulate the quantity or quality of afferent input at any stage of development and assess the functional and structural consequencies of such manipulations. Ideally, it would be desirable to be able to perform manipulations of afferent activity both in vivo and in vitro while the neuronal system is developing.

5. Direct access through peripheral receptor system. Since variations in the sensory environment can produce neuronal and behavioral modifications during development, it would be desirable if definable variations in afferent activity could be produced through these biologically relevant pathways.
6. Behavioral analog. To insure that the dimension along which afferent input is being manipulated in order to produce neuronal modifications is "biologically meaningful," it is desirable to determine if similar manipulations will produce functional changes in the organism's behavior.

Avian brain stem auditory pathways

The above considerations led us to the avian brain stem auditory system. Nucleus magnocellularis (NM) and nucleus laminaris (NL), which comprise 2nd- and 3rd-order auditory neurons, respectively, appear to be uniquely suited to investigations of the role of afferents in neuronal development and maintenance. Our initial investigations (RUBEL & PARKS, 1975; PARKS & RUBEL, 1975 and 1978) were primarily intended to provide detailed structural and functional information on the organization of this system. We then described the normal morphological development of NM and NL at the light microscope level (RUBEL et al., 1976). We are currently extending these observations with additional neurophysiological and morphological analyses of normal organization and development (SMITH & RUBEL, 1977; JACKSON et al., 1978). Finally, we have begun to describe how modifications of afferent input can alter the development and maintenance of the normal neuronal elements in this system (PARKS & ROBERTSON, 1976; PARKS, 1978; JACKSON & RUBEL, 1976; BENES et al., 1977; PARKS & RUBEL, 1977). In the following account we will briefly describe the results of some of these investigations. Our emphasis will be to demonstrate how the characteristics of this neural system make it appropriate for further analysis of the roles that afferent information may play in the ontogeny of neural structure and function.

The major avian brain stem auditory pathways, first described in detail by CAJAL (1908), are schematically shown in Figure 1. Axons of the cochlear ganglion cells enter the dorsolateral quadrant of the medulla and bifurcate into medial and lateral bundles. The lateral axon branches terminate in a cochleotopic manner in nucleus angularis (NA), which is composed of mixed cell types lying in the dorsolateral angle of the medulla. The medial branches of the VIIIth nerve fibers course along the floor of the fourth ventricle (IV) to terminate in NM. NM is a well-defined cluster of 3800—4200 large round or ovoid cell bodies which are either devoid of dendrites or have short, bushy, rudimentary dendrites. The cells are organized into dorsoventral columns with VIIIth nerve afferents coursing between the columns and terminating on the cell bodies as large endbulbs. Another input to the NM cells is of unknown origin, but may derive from axon collaterals of other NM cells (JACKSON et al., 1978). As shown in Figure 1, NL in chickens is composed of a discrete monolayer sheet of 1200—1600 cell bodies with bipolar dendritic orientations. NL cells receive binaural, spatially-segregated innervation from the magnocellular nuclei; axons from NM pass in the uncrossed dorsal cochlear tract to innervate the dorsal dendrites and cell bodies of the ipsilateral NL, and decussate in the crossed dorsal cochlear tract to innervate the ventral dendrites and cell bodies of the contralateral NL. No other inputs to NL have been observed. This

relatively simple structural organization, the accessibility of avian embryos for neurophysiological studies or peripheral manipulations, and the possibilities for precise control over the acoustic environment of embryos and hatchlings has warranted further investigation of the functional organization of NM and NL.

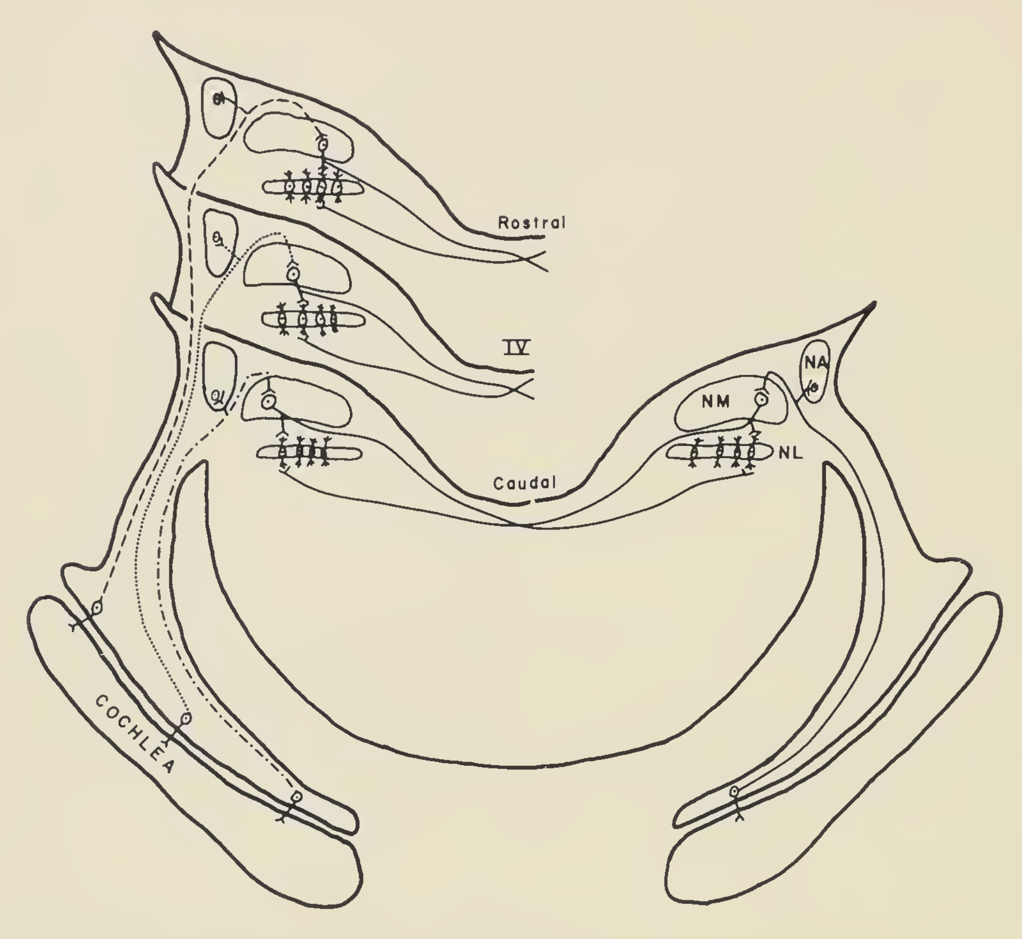


FIGURE 1. Schematic drawing showing the projections from the cochlea via the cochlear ganglion to n. angularis (NA) and n. magnocellularis (NM); and the spatially segregated, bilateral projections from n. magnocellularis to n. laminaris (NL). IV—4th ventricle (from RUBEL, SMITH & MILLER, 1976).

Neurophysiological examination of these nuclei and analysis of the projections from NM to NL revealed the following properties. NM cells respond only to a narrow range of frequencies played to the ipsilateral ear. The cells display sharp excitatory tuning curves, primary-type response histograms, and always have a definable characteristic frequency. Auditory nerve stimulation evokes only exitatory postsynaptic potentials with little convergence of auditory nerve fibers on individual NM cells. The cells form isofrequency columns, in which all cells respond to a similar characteristic frequency; the physiologically-defined columnar organization corresponds to anatomically observed cell columns. NL cells are binaurally activated by acoustic stimuli and usually show similar characteristic frequencies and thresholds to stimulation of each ear. That is, NL neurons are maximally activated by the same frequency range applied to either ear. In other respects, extracellular responses in NL are similar to NM neurons. Intracellular recordings display graded EPSP's of long duration. The organization of neurons in both nuclei is characterized by a highly stereotyped tonotopic organization; cells maximally responsive to low frequencies are situated in the caudolateral aspect of each nucleus and higher frequencies activate cells at progressively rostromedial positions. This tonotopic organization is sufficiently stereotyped that quantitative analyses

of the relationships between the position of a cell in each nucleus and its characteristic frequency allow accurate prediction of this functional characteristic (within 200—400 Hz) from positional information alone. The utility of this property is that it allows independent prediction of the normal characteristic frequency of a neuron, which can be compared to results obtained as a function of manipulations of a organism's acoustic environment.

By making small lesions in NM through tungsten microelectrodes after recording the characteristic frequency of cells in the lesioned area, and by both intracellular and extracellular injections of horseradish peroxidase, we have been able to further delineate the organization of the bilateral projections from NM to NL. There is a precise tonotopic and topographic projection from each region of NM to the dorsal side of ipsilateral NL cells and the ventral aspect of neurons in the corresponding position on the other side of the medulla. Furthermore, Golgi-stained tissue has revealed that the dendrites of NL cells are confined to the glia-free margin surrounding the cellular lamina and are qualitatively and quantitatively similar on the two sides of NL in any frequency region of the nucleus. These results allow precise delineation of the receptive cell surfaces of NL neurons as well as unusually precise specification of the source and functional properties of input to each dendritic surface of the neurons.

The first major morphogenetic event to be considered in the analysis of any neural region is the developmental stage and duration of time during which cellular proliferation occurs. Cumulative labeling with ^{3}H-thymidine can be used to determine the time at which cellular proliferation has ceased and the occurrence of heavy labeling is a good indicator that the time of isotope injection was during one of the final mitotic cycles. Our analysis of the brain stem auditory nuclei indicated that there is no overlap in the final period of DNA synsthesis between NM and NL. The majority of NM neurons leave the mitotic cycle between 48 and 72 hours of incubation, while the final division of NL cells occurs at about 84—100 hours of incubation. Both cell groups are produced in the region of the rhombic lip, and when first recognized in the 5—6-day embryo they overlap throughout most of their rostrocaudal and mediolateral extent. It is therefore reasonable to hypothesize that both cell groups are produces by a single progenitor population, with NM cells being formed first and migrating away from mother cells. Then, in a second wave of mitotic activity, the final population of NL cells is formed. This temporal sequence of cellular proliferation, coupled with the fact that NL cells come to lie directly ventral to NM, suggests that the cells may interact during their proliferative or migratory phases. Although there is little direct evidence for this hypothesis, we have observed that, at around 5—7 days of incubation, cells labeled at the same time as those of NL can be observed streaming through the magnocellular nucleus. The occurrence and possible functions of such interactions may be particularly susceptible to investigation in this system and may represent the first interaction between neurons which are destined to be functionally connected.

Following proliferation and migration, these cell groups develop their characteristic morphologies over the period from 9 to 15 days of incubation. By 9 days of incubation both cell groups can be easily recognized, although neither has assumed its mature cytoarchitectural or positional characteristics. At this stage, both nuclei are composed of relatively undifferentiated, densely-packed cell bodies and there is no apparent subnuclear organization. In silver-impregnated tissue, it is apparent that the major afferent

axons to both nuclei are present, although preliminary electron microscopic examination has revealed no synapses. Between days 9 and 13 major morphogenetic changes occur in both nuclei. The cells of NM are displaced medially, cell density diminishes, cell size increases, and the cells become aligned in their characteristic columnar organization. The most striking changes occur in NL, where, from the undifferentiated cluster of cells seen at days 8—9, a precisely defined monocellular or bicellular lamina, with a uniform glia-free margin, emerges by day 13. This change begins in the rostromedial portion of the nucleus between days 9 and 11 and is completed in the caudolateral portion by around day 14.

Changes in cell number occur in both nuclei concurrently with these morphogenetic events. Whereas NM loses only a few cells (0—20 %) and any cell death appears to occur between embryonic days 11 and 13, cell death in NL is much more extensive (about 70—80 %) and takes place over a considerably longer period (days 9—15). These changes in cell number are of interest for a number of reasons. First, while there are large differences in the amount and duration of cell death, the period of maximal cell loss in both nuclei is between 11 and 13 days of incubation. Since proliferation of NM and NL is separated by about 24—36 hours, it appears that whatever factors regulate cell death (see Levi-Montalcini, 1949; Cowan, 1973; Hamburger, 1975) may serve to bring the two nuclei into ontogenetic synchrony. Of possible importance in this regard is the fact that both physiological and behavioral studies indicate that the onset of afferent function is closely correlated with normal cell death. Current work on functional ontogeny in vitro will be of great importance for further understanding of this relationship.

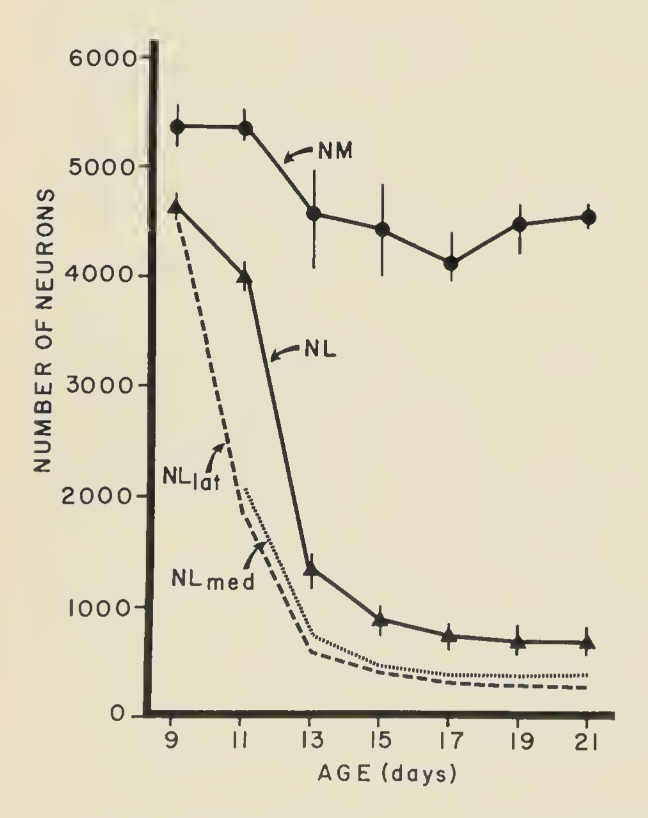


Figure 2. Cell counts in n. magnocellularis and n. laminaris from 9 days to hatching. Points are means for each time and vertical bars show ranges. Lines showing counts for the divisions of n. laminaris are mean values. NM, n. magnocellularis; NL, n. laminaris (total); NL lat., lateral division of n. laminaris; NL med., medial division of n. laminaris (from Rubel, Smith & Miller, 1976).

The volumetric analyses of NM and NL also indicate a surprising amount of developmental synchrony in the enlargement of cell bodies and neuropil areas which occurs after the period of cell death. Since it is quite likely that functional connection are established by day 15, it will be important to understand the role which afferent activity may play in the regulation of this parameter as well. It is therefore advantageous that

the period of rapid cellular and neuropil expansions can be temporally distinguished from that of cell death.

Summarizing the ontogenetic information, NM and NL display the following characteristics: i) the neurons of NM and NL go through their final phase of DNA synthesis over restricted and temporally separated periods, which allows independent labeling of either neuronal population; ii) the period of cell death does not overlap with the proliferative period; iii) the alignment of NL cells is temporally correlated with, and possibly results from, cell death; iv) cell loss occurs over a defined time period, has a definite spatial gradient and, in the case of NL, is quite extensive; and v) volumetric changes in cell bodies and neuropil regions occur in a period when functional connections are established and these changes occur following the time of maximal normal cell loss. These factors, in conjunction with the information on normal structural and functional connections, the access for experimentation afforded by the avian embryo, and the potential for controlling both the pre- and post-hatch acoustic environment suggest that these brain stem auditory pathways will serve as an excellent preparation for investigations of cell interactions in the developing nervous system.

Our first attempts at manipulating the cellular environment have used direct deafferentation. In one series of investigations (PARKS & ROBERTSON, 1976; PARKS, 1978; JACKSON & RUBEL, 1976) the effects of removing the VIIIth nerve afferents either prior to synaptogenesis (otocyst removal) or well after it (at hatching, three months, or three years) have been studied in NM. In agreement with LEVI-MONTALCINI (1949), it was found that removal of the otocyst had little or no effect on NM cell number or cell size until after 11 days of incubation, after which time both the amount and period of cell death were greatly enhanced. By 19 days of incubation, the deafferented NM had 40—50 % fewer cells than the normal population. Surprisingly, this effect was not age dependent; cochlea removal in hatchling, three-month-old, or adult chickens resulted in a similar amount of transneuronal cell loss in NM.

A second investigation (BENES et al., 1977) examined the degree to which transneuronal changes are specific to the postsynaptic membrane surface to which the input has been removed. By deafferenting one side of the NL cells it was possible to compare the deafferented dendritic surface with the other dendritic region of the same neurons, which had their normal input intact. An EM morphometric analysis revealed rapid and complete degeneration of the deafferented dendrites, while the opposite dendrites of these neurons retained their normal qualitative and quantitative characteristics.

While the total elimination of afferents to a neuron certainly interrupts more cellular processes than do changes in the pattern of synaptic activation, at least a portion of the deafferentation syndrome is probably due to the elimination of synaptic activity. Thus, the examination of developmental changes produced by total removal of afferents will yield a catalog of events, each of which can be systematically evaluated upon progressively more subtle manipulation of afferent activity. Furthermore, deafferentation results may form one end of a continuum relating the quality or quantity of afferent input to the integrity of neural structure and function. Most importantly, the avian auditory system will be valuable for testing of this and other hypotheses regarding the role of afferent activity in neural development. By controlling the sound environment it is possible to specify systematic variations in the activity impinging on known neuronal elements at any time after the receptor becomes functionally active. Furthermore, the

entire system as shown in Figure 1 is contained in a 1 mm slab of tissue and preliminary analysis (Jackson et al., 1978) indicates that it will remain viable in vitro over long periods. This quality may allow direct experimental control (via electrical stimulation) of the amount and pattern of activity in each auditory nerve at any stage of development.

Finally, with regard to the desirability of behavioral analogs, it should be noted that the ontogeny of auditory perceptual behavior can be readily studied in avian embryos and hatchlings (Gottlieb, 1970; Jackson & Rubel, 1978) and auditory deprivation can have marked effects on these behavioral processes (e.g., Gottlieb, 1976; Kerr et al., 1978).

While the above studies do not answer most questions of how the structural and the functional aspects of afferent input regulate neuronal ontogeny, we feel the avian brain stem auditory pathway still provides an excellent model for further investigation. It is hoped that progressively more subtle manipulation of afferent activity and increasingly sensitive measure of neuronal structure and function in this system will yield a more thorough understanding of how an organism's external environment regulates the ontogeny of neural networks.

Acknowledgments

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Response Properties of Avian Auditory-Nerve Fibers and Medullary Neurons

MURRAY B. SACHS, NIGEL K. WOOLF and JOAN M. SINNOTT

Introduction

Our long-term interest in the avian auditory system concerns the encoding of species-specific vocalization (SACHS et al., 1974; HIENZ et al., 1977; WOOLF & SACHS, 1977; SACHS et al., in press; SACHS & SINNOTT, in press). Because such vocalizations must contain acoustic elements of behavioral significance to the organism, they form an especially appealing set of stimuli with which to probe the nervous system. The avian auditory system has become the subject of intense study, and consequently the anatomical topology of its neural centers and their interconnections has become increasingly well understood (BOORD, 1969; KARTEN, 1967, 1968). Our approach to the study of stimulus encoding within the auditory system has been to characterize in detail the transformations which occur at the various levels within the system.

At higher central levels in the avian auditory pathway we have encountered complex properties in the stimulus-response relationships of single neurons. We have, however, attempted to identify the neural level at which the different response characteristics first emerge. In this paper we will discuss response properties of single neurons in the primary and secondary neural elements in the auditory pathway: the auditory nerve and the cochlear nuclear complex (n. magnocellularis and n. angularis). The experimental animal in these experiments is the Red-winged Blackbird *(Agelaius phoeniceus)*, studied under chloralose anesthesia.

Response properties of neurons in the avian auditory nerve

As in mammals, single fibers in the auditory nerve of birds exhibit spike discharge activity in the absence of controlled acoustic stimuli. The median spontaneous rate for the blackbird is about 90 spikes per second (WOOLF & SACHS, 1977), which compares with a median rate of about 30 spikes per second for the cat. This is consistent with our previous report that spontaneous activity in pigeon auditory-nerve fibers is considerably higher than that observed in the cat (SACHS et al., 1974). The most striking difference between the spontaneous rate distributions for birds and cats, however, is that the mode of the cat distribution occurs at rates of less than two spikes per second, whereas no avian fibers have demonstrated rates of less than two per second (SACHS et al., 1974; WOOLF & SACHS, 1977).

The temporal patterns of auditory nerve fiber responses to tones in birds appear quite similar to those reported for cat (KIANG et al., 1965). At the onset of a tone-burst, there is an increase in discharge rate; the response rate then decreases rapidly by 30—50 % over the next 50 msec and then decreases only very slowly for the duration of the tone-burst. Response patterns of this type are classified as "primary-like".

Department of Biomedical Engineering, Johns Hopkins University School of Medicine, Baltimore, Maryland, U.S.A.

The frequency selectivity of auditory-nerve fibers can be characterized in terms of a tuning curve, which is a plot of threshold of response to a tone versus frequency. The frequency at which the minimum threshold occurs is called the unit's "best frequency". One can characterize the sharpness of a tuning curve by a measure "Q", which is defined as the best frequency of a neuron divided by the bandwidth of the tuning curve 10 dB above the best frequency threshold. We have found that within the range of frequencies to which birds are sensitive, the Q's of their auditory-nerve fibers are quite similar to those in cats (SACHS et al., 1974; WOOLF & SACHS, 1977). This implies that cochlear filtering, which is directly reflected in the tuning of auditory-nerve fibers, is at least as sharp in the bird as it is in the cat. At sound levels above threshold, unit discharge rate rises monotonically to a maximum (saturation) level. Saturation rates for bird auditory-nerve fibers are significantly higher than those found in cat. Median saturation rate for the blackbird is about 300 spikes per second, as compared with 190 spikes per second for the cat (WOOLF & SACHS, 1977).

The threshold response level used in determining a tuning curve is usually a proportional increase above spontaneous rate in a fiber's average discharge rate. Average discharge rate, however, is a measure which does not account for fine temporal details in a neuron's response pattern. For example, it is well known that for low frequencies, auditory-nerve fiber spikes occur in temporal synchrony with individual cycles of a sinusoidal stimulus. This synchrony is conveniently displayed in a period histogram, which plots the number of spike discharges versus phase angle within a single cycle of the stimulus. The quantitative measure of the temporal synchrony in a unit's spike discharge pattern is refered to as its degree of "phase locking". The amount of phase locking occurring in these fibers is obviously one good measure of the ability of the peripheral auditory system to encode temporal features of a stimulus.

It is of interest to compare the temporal coding in birds with that in mammals. JOHNSON (1974) has shown that the amount of phase locking in cat auditory-nerve fibers decreases in approximately inverse proportion with frequency above 1 kHz. We have shown that in blackbirds precisely the same relationship exists (WOOLF & SACHS, 1977). Thus, the ability of the avian peripheral auditory system to encode stimuli temporally is apparently the same as that of the cat, for frequencies greater than 1 kHz. Phase locking to frequencies below 1 kHz may be somewhat better in birds than in cats (WOOLF & SACHS, in preparation).

Response properties of neurons in the avian cochlear nucleus

In birds, the auditory-nerve bifurcates upon entering the central nervous system, and projects onto two spatially discrete medullary nuclei: nucleus magnocellularis and nucleus angularis. These have been considered to be homologous to the mammalian anteroventral cochlear nucleus and the posteroventral and dorsal cochlear nuclei, respectively (BOORD, 1968, 1969).

Nucleus magnocellularis exhibits rates of spontaneous activity comparable to those observed in the auditory nerve. Median spontaneous rates for n. magnocellularis in the blackbird are approximately 110 spikes per second (SACHS & SINNOTT, in press). Nucleus angularis, on the other hand, is characterized by having a large proportion of units

with low spontaneous rates. Approximately 30 % of units in blackbird n. angularis have spontaneous rates of less than 10 per second (SACHS & SINNOTT, in press).

Nucleus magnocellularis also appears similar to the auditory-nerve in the temporal patterns it displays in response to tones. Both exhibit only "primary-like" responses. Nucleus angularis distinguishes itself by the occurrence of units with onset or pauser type responses, in addition to "primary-like" responses.

For central neurons the organization of excitatory-inhibitory response areas in the frequency-pressure plane is displayed in terms of a unit's "response map". Excitatory areas are defined as regions in the frequency-pressure plane where tones cause an increase in average rate of at least 25 % above spontaneous rate; inhibitory areas are regions where tones cause a decrease of at least 25 % below spontaneous rate. Both the auditory-nerve and n. magnocellularis exhibit response maps characterized by a central excitatory V-shaped region, where tones at best frequency are excitatory at all levels above threshold. In n. magnocellularis, inhibitory regions always flank the excitatory areas on one or both sides. This "simple" type of response map is also found in 90 % of the units in n. angularis (SACHS & SINNOTT, in press).

In addition to this type of response map, about 10 % of the units in n. angularis exhibit "complex" response maps. These include maps in which the excitatory best fre-

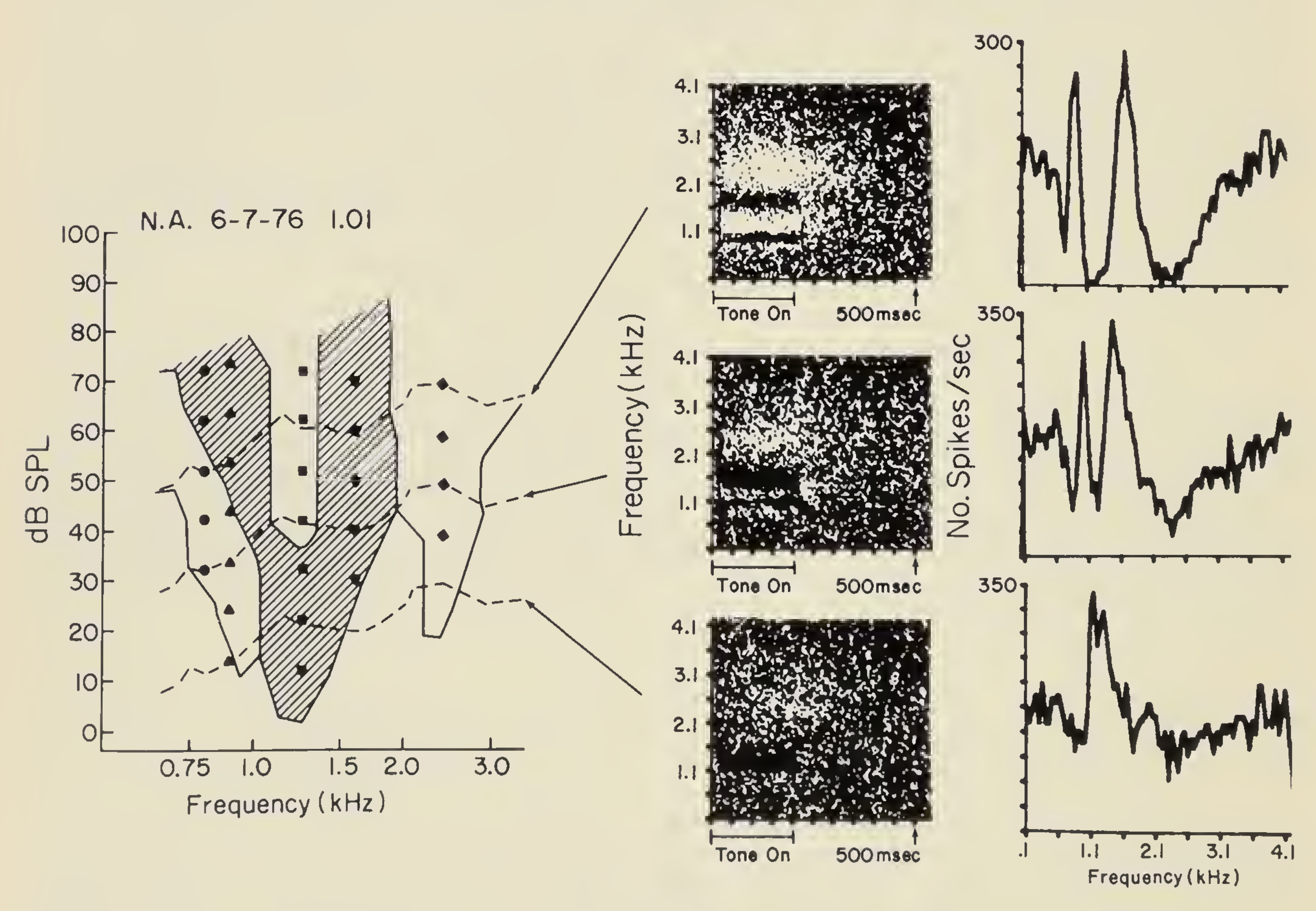


FIGURE 1. Response map for a type IV unit from Nucleus angularis is shown on left. At center are dot displays showing responses to probe tones at three different levels. Each line in the display gives responses to the frequency given by the ordinate. For each dot display, the voltage into the earphone is constant, but the resulting acoustic calibration is not flat and is indicated by a dashed line in the response map. The arrows point to plots of sound level at the eardrum versus frequency for this corresponding earphone voltage. The calibration plots are helpful in relating the probe analysis data to the detailed response map made with a different technique. At right are shown the discharge rate versus frequency plots for the probe analysis data.

quency at threshold gives way to inhibition at higher intensities (type IV units of Evans & Nelson, 1973; Young & Brownell, 1976). These inhibitory regions at higher levels extend to frequencies both above and below best frequency. Excitatory areas are also observed at higher levels; in some cases these are continuous with the excitatory area near best frequency, while in other cases they are isolated. The resulting interleaved arrangement of excitatory and inhibitory response areas can be quite complex; at a fixed sound level above threshold, the response of a unit can change from inhibitory to excitatory and vice-versa several times as frequency is changed from low to high (e.g., see Fig. 1).

Discussion

When we consider measures of spontaneous activity, types of response patterns, and types of response maps in the auditory nerve and cochlear nuclei, we can conclude that the auditory nerve and n. magnocellularis function rather similarly (i.e., high spontaneous rates, simple response maps, and primary response patterns). Nucleus angularis, however, stands out as capable of more complex degrees of stimulus encoding. This is reflected by a significant population of units having low rates of spontaneous activity, a variety of different types of response patterns (i.e., pauser and onset patterns as well as primary types), and complex as well as simple response maps.

At higher levels of the auditory system, units are frequently characterized by complex response maps. Some of these complex neurons exhibit rate versus frequency plots similar to those of type IV units which occur for the first time in n. angularis of the cochlear nucleus (Scheich et al., 1977). Thus, it appears likely that some of the properties of complex neurons observed can be directly related to properties of neurons in lower centers.

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Functional Organization of Auditory Centres in the Midbrain of Birds

R. B. Coles

Extracellular recordings were made from auditory units in the midbrain of the anaesthetized (Equithesin) domestic fowl *(Gallus gallus)*. The dorsal regions of the optic lobe were exposed by removing part of the overlying caudal forebrain. Glass microelectrodes (filled with 2M NaCl and Pontamine blue dye) were then inserted, under direct visual control, into the superficial layers of the optic tectum. Unit recordings were then continued remotely, outside the sound-attenuated chamber containing the preparation. Recording sites were strategically marked in the midbrain by injection of dye from the electrode tip (by current), in order to accurately reconstruct each electrode penetration histologically. Using this procedure the principal auditory area of the midbrain of the domestic fowl was clearly determined to be the nucleus mesencephalicus lateralis pars dorsalis (NMLD).

The functional properties of NMLD cells were studied using monaural and binaural sound stimuli, presented as repetitive bursts (10 msec. rise/fall time; 300 msec. plateau duration) consisting of pure tones and sometimes frequency-modulated (FM) tones. Sound intensity was calibrated by using on-line probe systems incorporated into the sound delivery tube at each ear. Unit recordings were analysed with peri-stimulus time (PSTH) or interval (IH) histograms, using an off-line computer system. Using contralateral pure tone bursts, 84 % of NMLD cells were found to be predominantly excited (transient and/or sustained responses). Excitatory tuning properties with familiar V-shaped threshold curves were produced from contralateral stimulation. A very restricted frequency response range, at the most sensitive intensity thresholds could be determined (best frequency or BF) for most NMLD cells. However more complex tuning properties were also evident from monaural stimulation (12 %) and such cells displayed various forms of broad tuning (inhibitory sidebands, double sensitivity peaks and FM sensitivity). Most NMLD cells (69 %) had BF's between 750 Hz and 3.0 kHz and the most sensitive BF thresholds occurred between 1.0—2.0 kHz (see Fig. 1).

The minimum loss in unit BF threshold below 1.0 kHz was approximately 16 dB/octave, compared to a substantially greater loss (46 dB/octave) above 2.0 kHz. Due to this rapid loss in high frequency sensitivity for NMLD cells, the highest BF's did not exceed 5.0 kHz, although responses up to 7.0 kHz could be elicited from very intense tones (100 dB SPL). The lower frequency limits for NMLD cells were more difficult to establish since responses were detected at least as low as 40 Hz (limit of sound system),but at high intensities for air-borne sound (above 60 dB SPL). It is possible that at sufficiently low frequencies, some non-auditory vibration sensitive system may have been stimulated by the sound system. In addition, phase-locked responses were very prominent for frequencies between 40—500 Hz; however above about 800 Hz this type of response pattern was increasingly difficult to detect.

Monaural inputs to NMLD cells were further examined and call types were classified as contralateral excitation coupled with either, ipsilateral inhibition (EI, 46 %), exci-

Monash University, Melbourne, Australia.

tation (EE, 21 %) or no effect (EO, 17 %). When examined on the basis of BF distribution, EI cells occurred most frequently between 400 Hz and 4.0 Hz. The BF's of EE cells, although showing a similarly wide distribution, indicated some preference for frequencies below 1.0 kHz. In contrast the BF's of monaural EO cells demonstrated a distinct bias towards high frequencies, usually above 1.0 kHz.

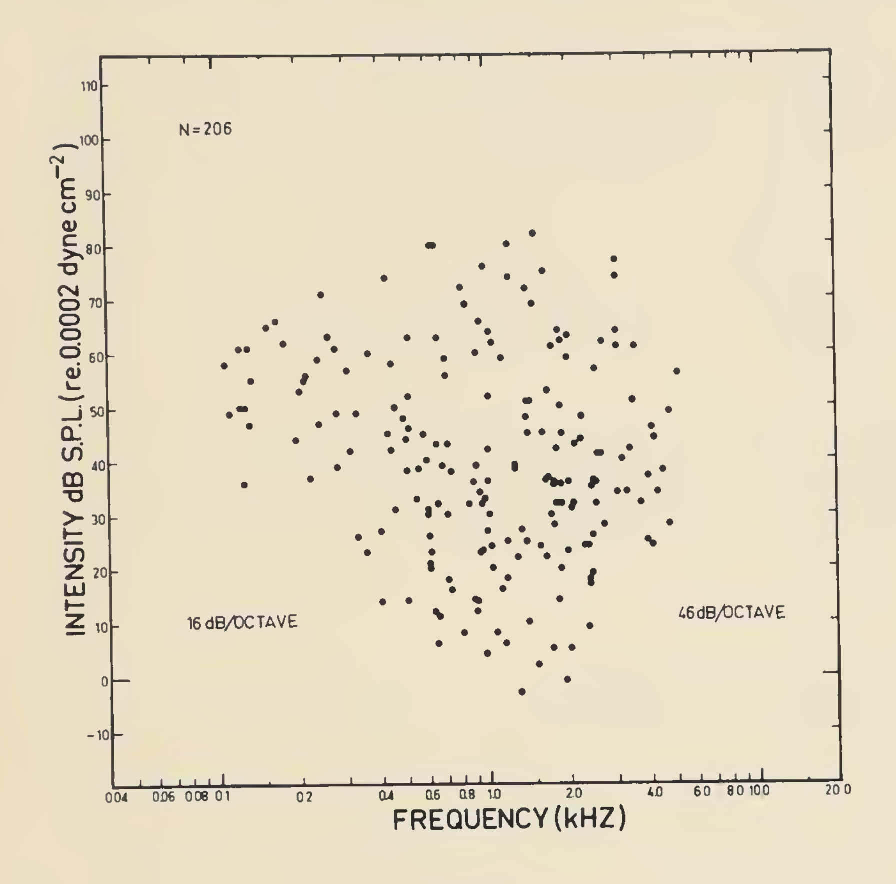


Figure 1. Distribution of unit best frequency (BF) thresholds for 206 cells from the NMLD of the domestic fowl.

EI and EE cells were tested with experimentally produced differences in interaural time (ITD) and intensity (IID), in order to study their possible involvement in the neural processes of sound localization. EI cells were found to be quite sensitive to changes in interaural intensity in the range of 5—20 dB when tested above threshold at their BF. Some EE cells were found to be sensitive to ITD but such sensitivity, although cyclic, usually occurred over several milliseconds of interaural delay. ITD sensitivity appeared to be a function of stimulus periodicity (below 800 Hz), since in such cases these EE cells appeared to respond in a phase-locked manner to monaural acoustic stimuli. A consideration of the physical binaural disparities for the head of the domestic fowl would suggest perhaps a maximum of only 60 µsec for ITD (based on ear separation), and also the maximum IID would probably not exceed 10 dB even for the highest audible frequencies available to the domestic fowl (due to head shadow). The response properties of binaural cells in the midbrain of domestic fowl would suggest that delay-sensitive EE cells are extremely insensitive to expected physical ITD's. However EI cells have a sensitivity to IID, presumably within the range encountered in the normal acoustic environment of this bird. Thus the neurophysiological evidence presented in this study would favour the use of frequency-dependent binaural intensity differences as possibly the only effective cue during sound localization in the domestic fowl.

The histological reconstruction of electrode tracks through regions of the NMLD enabled the organization of auditory unit responses to be accurately determined. Unit BF's in the NMLD were found to be very strictly organised in the vertical plane, such

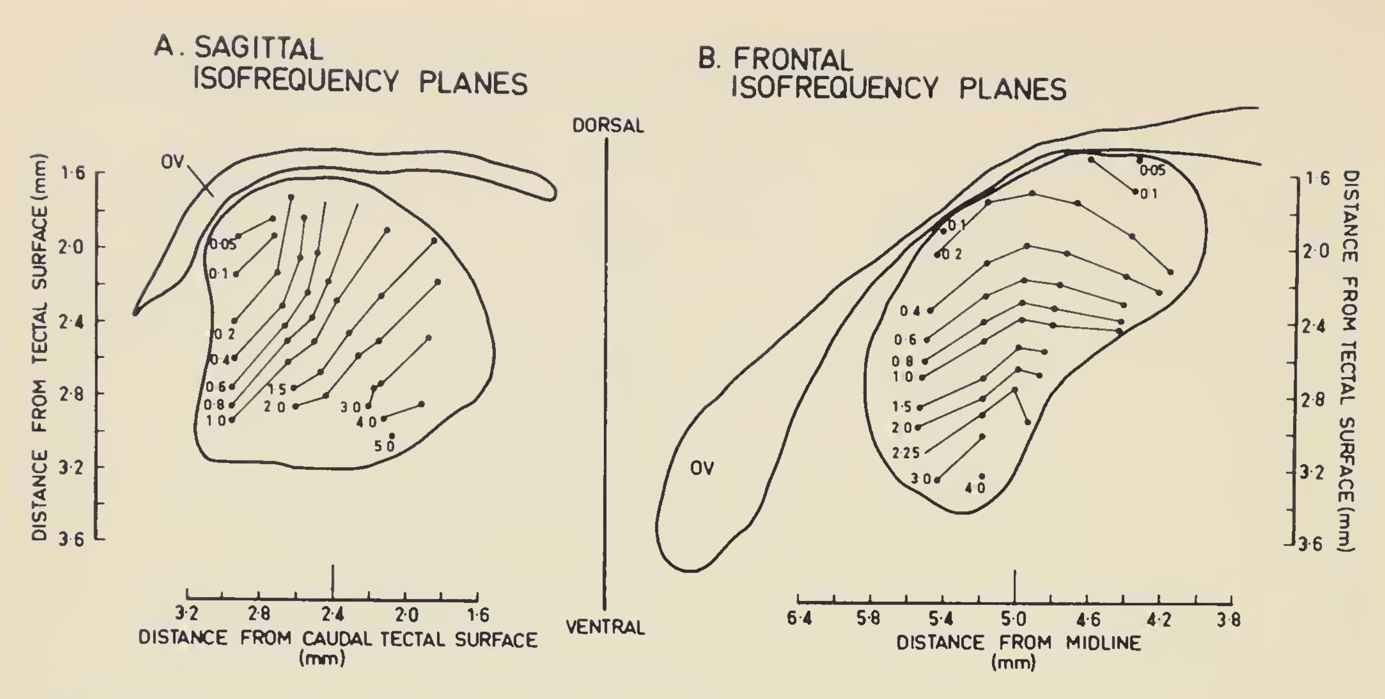


FIGURE 2. Construction of iso-frequency planes from vertical electrode penetrations into the NMLD (combined from separate experiments). Data points of equal BF (kHz) have been connected to indicate orientation of the planes for a representative section of the NMLD (see extended line on each abscissa).

that tonotopic sequences of increasing BF occurred when electrodes were advanced in a dorso-ventral direction. Low frequency cells were found mostly in the dorso-rostral and dorso-medial regions of the NMLD, where such responses were typically phase-locked, including responses below 100 Hz in the extreme medio-rostral part of the NMLD. Iso-frequency planes were constructed by correlating unit BF's with depth in the NMLD (see Fig. 2).

These planes extended from 50 Hz up to 5.0 kHz, with high frequency responses occurring latero-ventrally (frontal plane) and caudo-ventrally (sagittal plane). Tonotopic organization was also indicated for the horizontal plane. Thus the NMLD may be regarded as functionally laminated, probably consisting of a series of concentric arcs radiating dorso-rostrally (low frequencies) to ventro-caudally (high frequencies) in the sagittal plane. In the frontal plane these laminae mostly extended parallel to the slope of the optic ventricle.

A second auditory region in the midbrain was identified as part of the sub-ventricular extensions of the stratum griseum (et fibrosum) periventriculare (SGP). Most auditory units in the SGP (usually fibres) originated from the thin capsular extension immediately dorsal to the NMLD, and were frequently broadly tuned and showed habituation to repeated stimuli. A weak, reversed tonotopic sequence of unit BF's (relative to the NMLD) was present in the SGP. Occasionally auditory units were also isolated in the SGP immediately above the optic ventricle i.e. in the optic tectum itself. The location of such units suggests the possibilities for audio-visual (and somatosensory) interactions. In rare cases auditory units were found in areas immediately ventral to the NMLD (not associated with lateral lemniscal input) corresponding to part of the formatio reticularis lateralis (FRL). Units located in the nucleus intercollicularis (ICo) did not respond to auditory stimuli and the functional boundary for auditory units appeared to correspond to the anatomical boundary (from NISSL staining) between the

NMLD and the ICo. Under the present experimental conditions this result supports the idea of a segregation of function in the midbrain of the domestic fowl between the NMLD, being a major afferent acousto-sensory area, and the ICo, an important acousto-motor (vocal) area.

Sound Localization on the Neuronal Level

ERIC I. KNUDSEN

Birds perform a wide variety of acoustically guided behaviors including prey capture, predator avoidance and various forms of social communication that place a demand on the ability of their auditory system to localize sound sources in space. However, the auditory sense organ, the cochlear partition, is essentially a one-dimensional sensory surface that responds differentially to sound frequency along its length, but that receives no direct spatial information from the acoustic environment. Thus the auditory system must derive the location of a sound source from the relative patterns of auditory nerve input arriving from the two ears. This is a considerably more complex task than that demanded of the visual or somatosensory systems, for which spatial information is immediately available at the sensory surface. Nevertheless, it is apparent from the sound localization abilities of many birds (ENGELMAN, 1928; GRANIT, 1941; SCHWARTZKOPFF, 1950; PAYNE, 1971; KONISHI, 1973) that their auditory systems can accurately determine the direction of sound sources. The Barn Owl *(Tyto alba)*, for example, can locate a sound source to within 2° in both azimuth and elevation (KNUDSEN & KONISHI, in preparation), an ability that allows this bird to hunt efficiently even in total darkness. This paper will describe how single neurons in the auditory system of the Barn Owl encode such 2-dimensional spatial information in a form that may directly underlie behavioral sound localization.

The experimental strategy was to study the influence of sound location on the response properties of auditory neurons by using a movable sound source in an acoustic free-field. Neuronal responses were looked for that depended upon the location of the sound source, but that were relatively independent of the type of sound used.

The experiments were conducted with the owl placed in a large anechoic chamber. The free-field sound source was supplied by a 5-cm speaker that could be moved by remote control from outside the chamber (KNUDSEN et al., 1977). The speaker moved along a semicircular track (1 m radius) to provide changes in sound azimuth, and the track itself pivoted around a horizontal axis to provide changes in sound elevation. Thus the speaker could be positioned anywhere around the owl on a sphere of radius 1 m, except for a 20° sector blocked by a supporting post for the owl. Sound stimuli included noise bursts, tone bursts, and clicks.

Seven owls were used in these experiments, each owl being prepared for chronic recording (KNUDSEN & KONISHI, 1978b). Anesthesia was induced with an intramuscular injection of ketamine hydrochloride, and was maintained at a light level with repeated injections as necessary. The anesthetized owl was secured to a holder and was positioned at the center of the sphere described by the movement of the speaker. The owl's head was oriented by exploiting retinal landmarks so that its visual and median planes corresponded to 0° elevation and 0° azimuth of the speaker (Fig. 1).

The neuronal properties that will be described here are based on the responses of 149 units located in the midbrain auditory area known as mesencephalicus lateralis

Division of Biology, California Institute of Technology, Pasadena, California, U.S.A.

dorsalis (MLD), as determined by histological reconstruction. The units were recorded with glass-insulated tungsten electrodes; conventional amplification and spike analysis equipment was used.

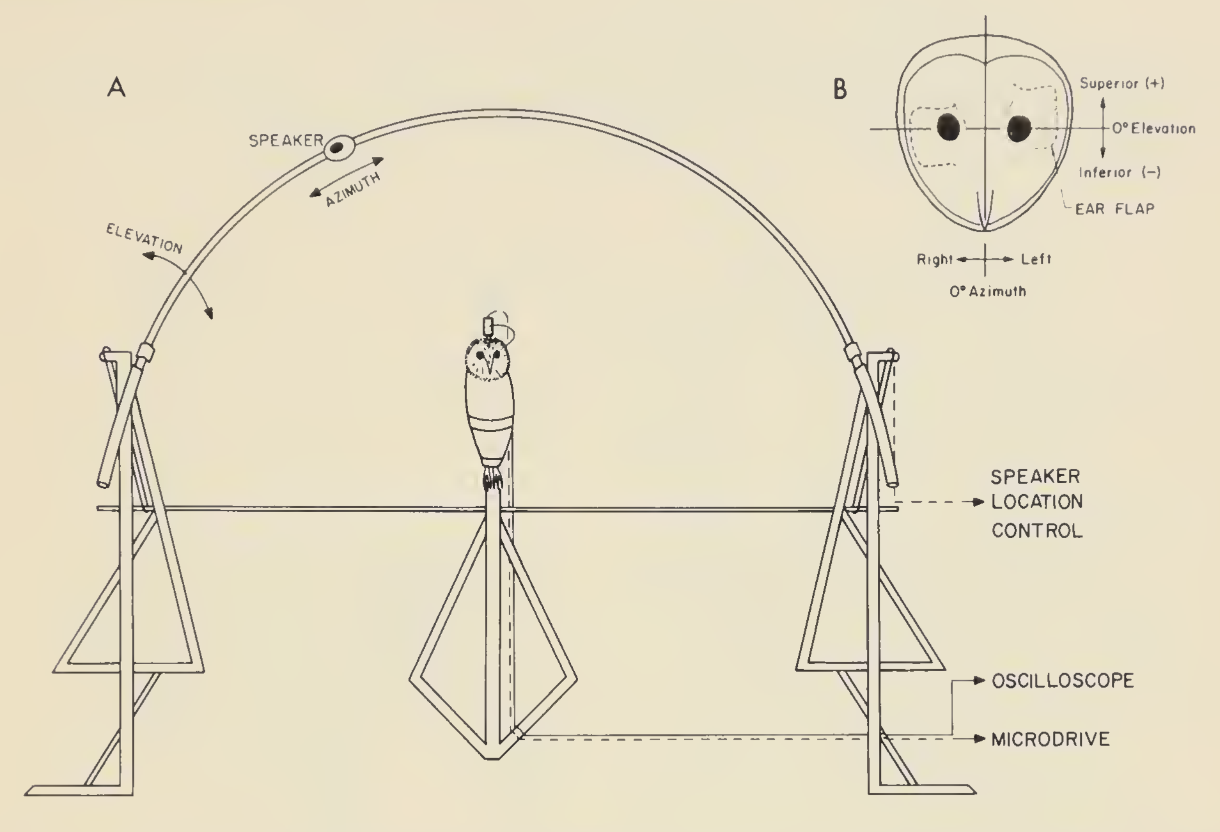


FIGURE 1. The experimental apparatus and the division of auditory space with respect to the owl's head. A: An owl is depicted in testing position at the center of the spaker-carriage system, which is located inside the anechoic chamber. The speaker location control, oscilloscope, and hydraulic microdrive are located outside the chamber. B. Auditory space was divided with reference to the owl's median and visual planes. Speaker locations across the median plane from the side recorded were measured in contralateral degrees (x_c°), on the same side were ipsilateral degrees (x_i°). Above the visual plane were positive degrees ($+y^\circ$), below were negative degrees ($-y^\circ$). (From KNUDSEN & KONISHI, 1978b).

Receptive fields of auditory neurons

MLD units respond to sound source location in a variety of ways. One class of units responds similarly to a sound stimulus regardless of its location. A second class of units responds best to sound from a particular area of space, but the borders of this area expand considerably with increasing sound intensity. A third class of units is excited by sounds from several discrete areas of space, and inhibited by sound sources located between these areas. A fourth class of units responds to sound only when it originates from a single restricted area of space, or receptive field. It is this fourth class of units, called limited-field units (L-F units), that will be discussed in this paper.

The receptive fields of L-F units were plotted in the following manner. After a single unit was isolated, the speaker, while emitting noise bursts, was moved to a location to which the unit responded vigorously. With the speaker at this location the threshold of the unit to noise bursts was determined. The intensity of the noise bursts was then increased to 10 dB above threshold and the speaker was moved in azimuth and elevation to positions where the unit just failed to respond. The coordinates of these positions defined the borders of the unit's receptive field.

The receptive fields of L-F units (Fig. 2) are in the shape of vertically oriented ellipsoids (94 %, 140 out of 149) or occasionally bands (6 %), and range in size from 5° to 40° (average 23°) in azimuth, and from 18° to "unrestricted" in elevation. Within each receptive field is a small area to which the unit is most responsive. As the sound source moves away from this area, the response of the unit declines markedly. This area, called the unit's best-area, ranges in size from 2.5° to 10° in azimuth and from 5° to 45° in elevation.

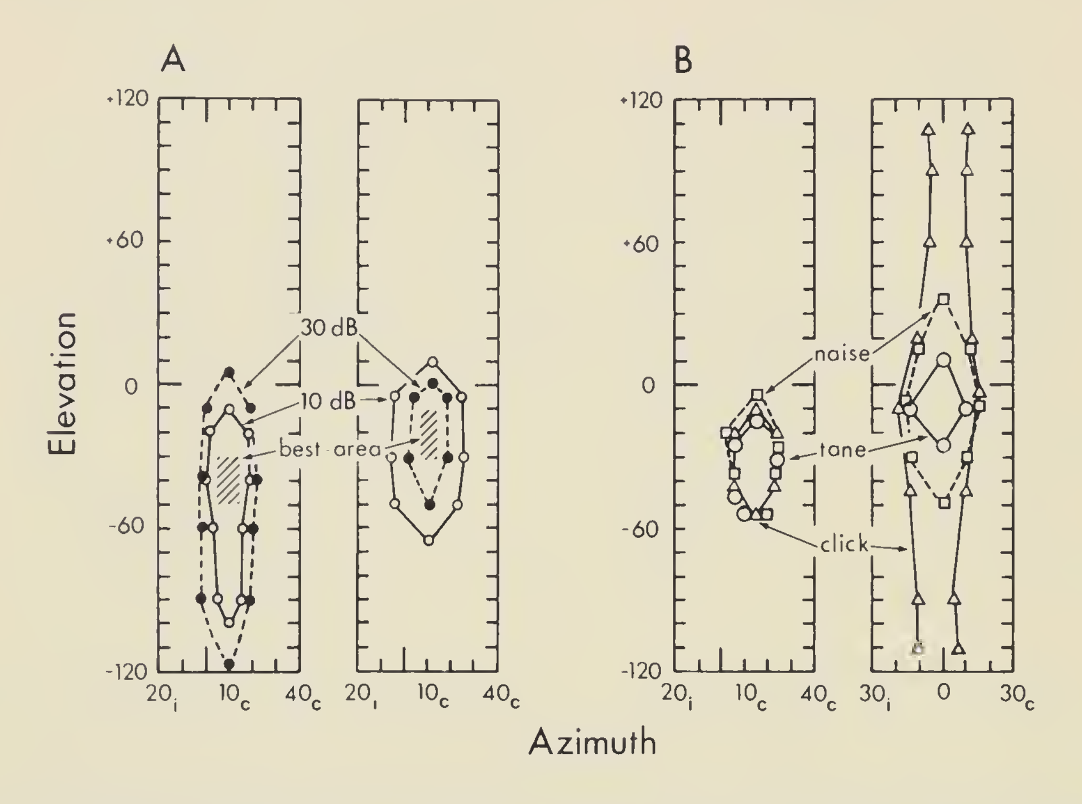


FIGURE 2. The effect of sound intensity and sound type on the receptive field plots of limited-field units. A: The receptive fields of two units plotted with wide-band noise bursts at 10 dB (open circles) and 30 dB (closed circles) above threshold. The field of the unit on the left expands, and the one on the right contracts at the higher sound intensity. B: The receptive fields of two units plotted with noise bursts, CF-tone bursts, and clicks, each presented at 30 dB above threshold. The unit on the left is typical of limited-field units. The unit on the right represents the most extreme case of receptive field variation due to sound type. (From KNUDSEN & KONISHI, 1978b).

An impressive characteristic of these auditory receptive fields is their insensitivity to large increments in sound intensity (Fig. 2a). When receptive fields plotted at 30 dB above threshold were compared with those plotted at 10 dB above threshold for 87 units, 48 % changed in azimuth by only 2° or less, 34 % expanded by 3°—11°, and 18 % actually contracted by 3°—18°. Insensitivity to such large changes in sound intensity cannot be explained by the directionality of the owl's ears (PAYNE, 1971; KNUDSEN & KONISHI, 1978b), especially in those cases where the receptive fields become smaller at the higher sound intensity. Clearly some form of space-dependent neuronal processing must occur to prevent these units from being stimulated by sounds that originate outside their receptive fields.

Another important property of these units is that their receptive fields are little affected by the type of sound used for mapping (Fig. 2b). Receptive fields mapped using clicks or tone bursts at characteristic frequency (CF, the frequency to which a unit responds with lowest threshold) exhibit the same best areas and approximate fields boundaries as those mapped with noise bursts. Thus these MLD units respond to a

fairly wide range of sounds as long as the sound source is located inside their receptive fields.

Spatiotopic organization of receptive fields

The impression that L-F units are involved in spatial analysis of sound is reinforced by their distribution and functional organization in MLD. L-F units are found exclusi-

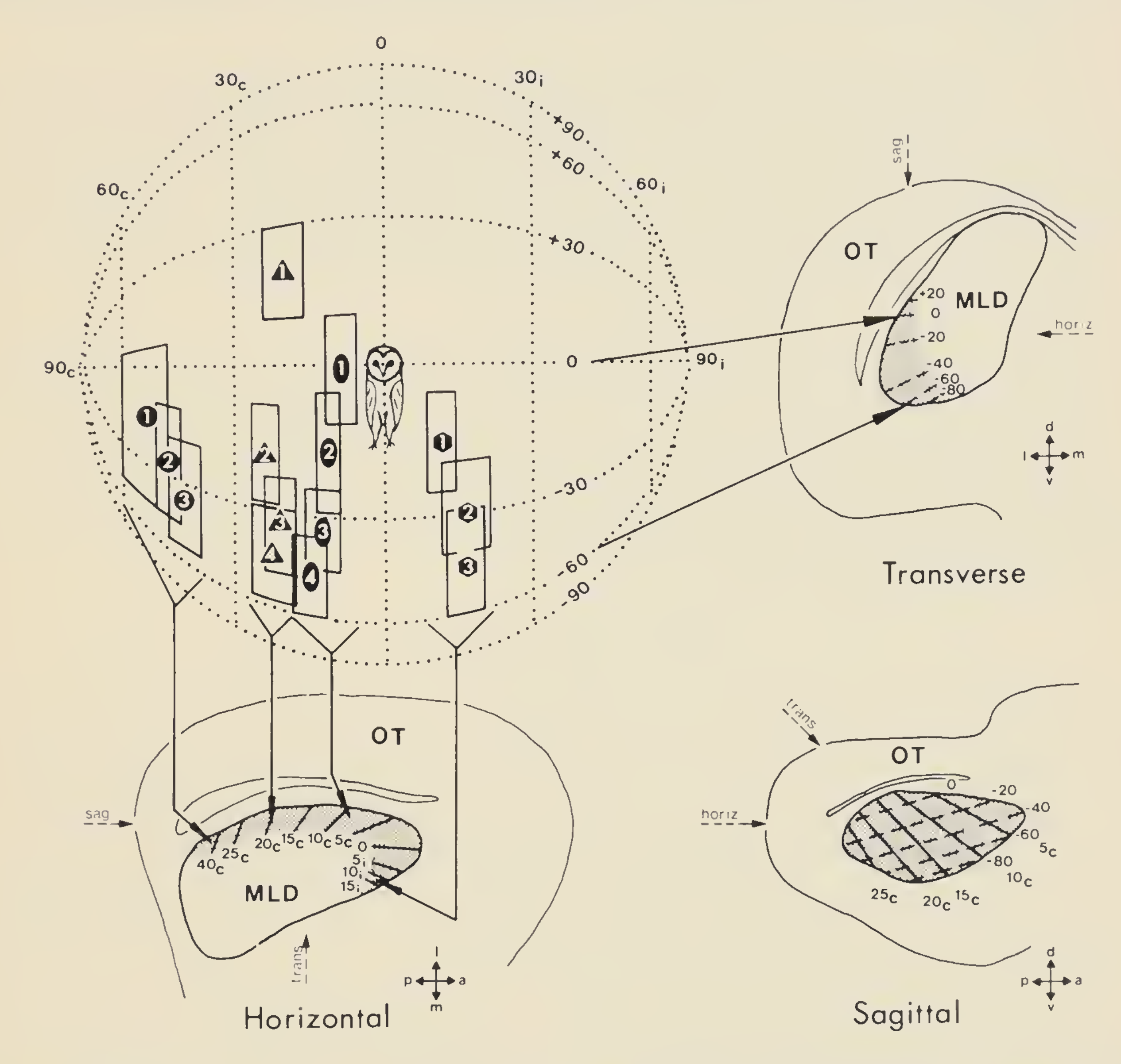


FIGURE 3. The representation of auditory space in the midbrain nucleus (MLD), as defined by the center of unit best-areas. In the upper left the coordinates of auditory space are depicted as a dotted globe surrounding the owl. Projected onto the globe are the best-areas (solid-lined rectangles) of 14 units that were recorded in four separate penetrations. The large numbers backed by similar symbols represents units from the same penetration; the numbers themselves signify the order in which the units were encountered, and are placed at the centers of their best-areas. The penetrations were made with the electrode oriented parallel to the transverse plane at the positions indicated in the horizontal section by the solid arrows. Below and to the right of the globe are illustrated three histological sections through MLD in the horizontal, transverse, and sagittal planes. The stippled portion of MLD corresponds to the space-mapped region; the remaining portion is the tonotopic region. Isoazimuth contours, based on best-area centers, are shown as solid lines in the horizontal and sagittal sections; isoelevation contours are represented by dashed lines in the transverse and sagittal sections. On each section dashed arrows indicate the planes of the other two sections. Solid, crossed arrows to the lower right of each section define the orientation of the section: a, anterior; d, dorsal; l, lateral; m, medial; p, posterior; v, ventral. The optic tectum (OT) is labeled on each section. (From KNUDSEN & KONISHI, 1978a).

vely along the lateral and anterior margins of MLD (KNUDSEN & KONISHI, 1978a). Within this region they are systematically arranged according to the azimuths and elevations of their best areas to form a physiological map of auditory space (Fig. 3). This map is oriented so that sound azimuth is represented in the horizontal plane, and sound elevation is represented in the transverse plane of the nucleus. Thus in a typical electrode penetration, made dorsoventrally and in the transverse plane, the best areas of sequential units shift continuously in elevation from high to low, while changing little in azimuth.

Most of the map is devoted to contralateral auditory space (Fig. 3). Best area centers extend in azimuth from 60° contralateral (60°_c) represented in the posterolateral corner, to 15° ipsilateral (15°_i) represented in the anteromedial corner, and in elevation from 20° above the visual axis (+20°) dorsally, to 90° below the visual axis (−90°) ventrally. Notice also that the area of space from 20°_c to 0° in azimuth and from −10° to −60° in elevation is represented by a disproportionately large volume of tissue in this map.

It is important to keep in mind that this auditory map of space has been synthesized from neuronal inputs that are not intrinsically spatially organized. Instead, the auditory system must derive its receptive fields and sensory map from the patterns of auditory nerve input arriving from the two ears. In this respect, the auditory map of space is an emergent property of central integration, distinguishing it from all other sensory maps that are direct projections of the sensory surface.

Behavioral implications

Because the map and the space-dependent response properties of L-F units must be generated through neuronal integration, it seems likely that this specialized region of MLD is intimately involved in the analysis of spatial aspects of auditory signals. Assuming that this region does in fact participate in behavioral sound localization, then its functional characteristics and limitations should be manifest in the localization abilities of the owl. For example, (i) The vertically elongate shape of the receptive fields implies that the owl's elevational acuity is poorer than its azimuthal acuity. (ii) The map of auditory space suggests that the owl can localize even a brief sound without head movement. This prediction contradicts PAYNE's (1971) theory of sound localization, in which the owl supposedly localizes sound by turning its head until the intensity of all frequencies is maximized in both ears. (iii) The emphasis given by the map to the inferior-frontal area (±20° in azimuth and −10° to −60° in elevation) predicts that the owl's angular acuity is maximal within this area and drops off rapidly as the location of the sound source becomes more peripheral. Behavioral experiments are now being conducted to test these predictions.

Acknowledgements

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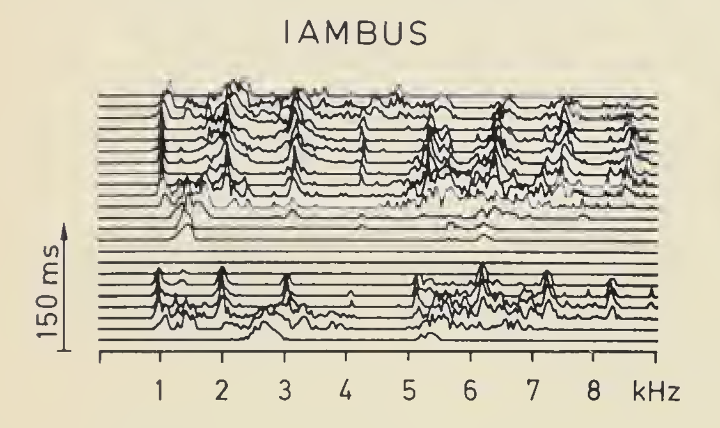
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Auditory Midbrain and Forebrain Units in the Guinea Fowl *(Numida meleagris)*: Degrees of Specialization for Focal Properties of Calls

H. Scheich

Birds communicate to a great extent with sound patterns. Most remarkable in a comparative survey of vocalizing vertebrates is the large size of vocal repertoires of many bird species, even if song is not taken into account (Marler, 1977). The Guinea Fowl uses some twenty call types which convey different information (Maier, 1977). These calls are acoustically complex. Their "building blocks" are only a very few acoustic dimensions which are modified or recombined so that always some call types share certain characteristics besides having unique features.



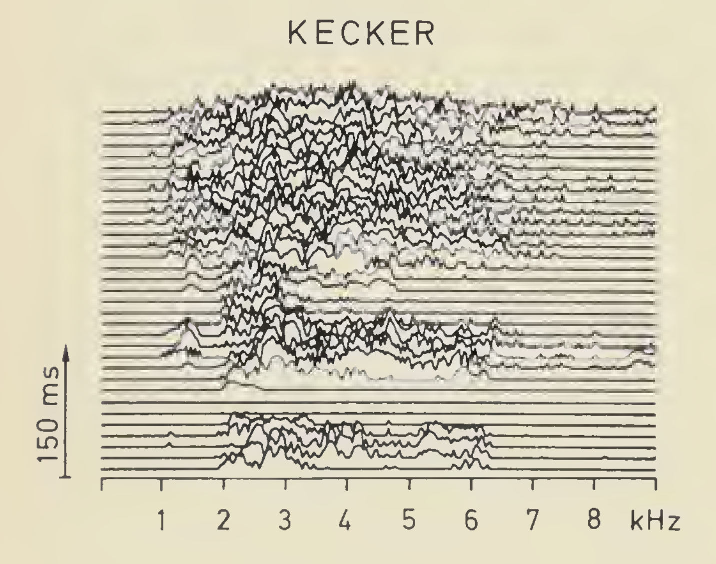


Figure 1. Power spectra of a Iambus and of a Kecker call. The calls are Fourier-analyzed in sections of 15 ms duration with some overlap. The time runs from bottom to top.

Note the harmonic spectrum of the Iambus with inconsistent sidebands. The Kecker call (two short and a long element are shown from a longer series) is built from higher harmonics of about 300 Hz which are obscured by additional noise.

It appears interesting to determine what strategies are used by the bird auditory system to distinguish and recognize calls with the above properties. Most significant for pattern recognition seems to be the presence of prominent auditory midbrain (MLD) and forebrain areas (Auditory Neostriatum) in birds (Karten, 1967, 1968; Bonke & Scheich, in prep.).

Institut für Zoologie der Technischen Hochschule Darmstadt, Schnittspahnstr. 3, D-6100 Darmstadt, Bundesrepublik Deutschland.

There is recent evidence that the neostriatum in songbirds (LEPPELSACK & VOGT, 1976) and in gallinaceous birds (SCHEICH, 1977) harbours at least 10 % neurons which respond in a highly selective fashion to calls of the species. The conclusion on selectivity of single neurons has been reached by comparing the responses to various calls of the species.

Neuronal discrimination may be trivial if calls, responses to which are compared, have no or little spectral content in common. Discrimination is highly interesting, however, if calls are distinguished which have largely common frequency bands.

This is the case with the Iambus of the Guinea Fowl, a hen call, which facilitates cohesion between a hen and her mate and with the Kecker, which is uttered by males and females upon disturbances in the environment (MAIER, in prep.). The Iambus consists of two notes (Fig. 1). The spectrum typically shows lines at about 1 kHz with strong harmonics and with inconsistent sidebands about 300 Hz above and below the

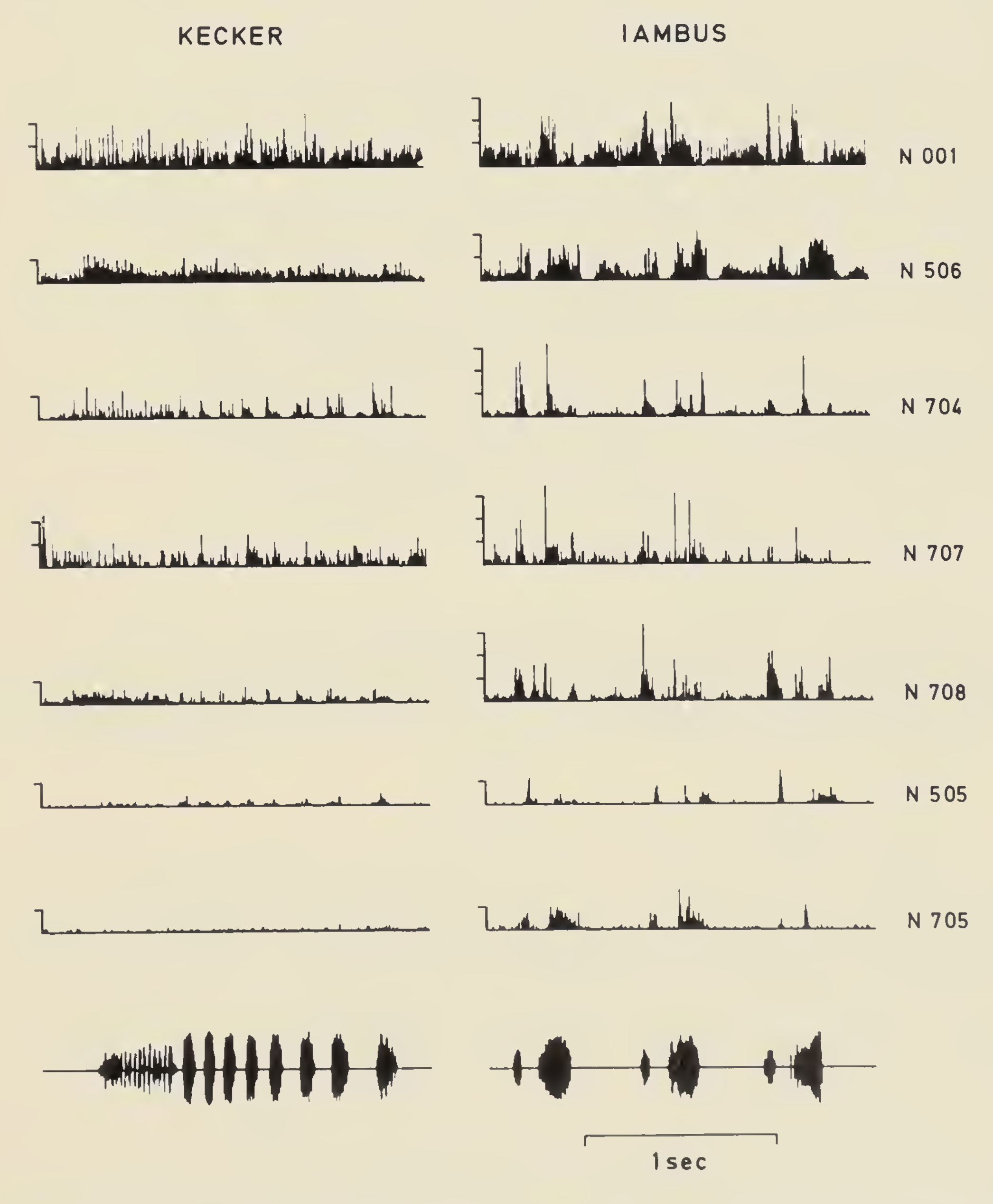


FIGURE 2. Responses of seven MLD units which distinguish quantitatively (with one exception) between Kecker and Iambus. The stimuli, a series of long and short Kecker pulses and three Iambi, were repeated 20 times and are shown below. Note the high temporal precision of firing (5 ms binwidth of the PSTH) and the multiple peaks of activity during the presentation of the call. Scale divisions on the ordinate indicate 50 spikes/bin.

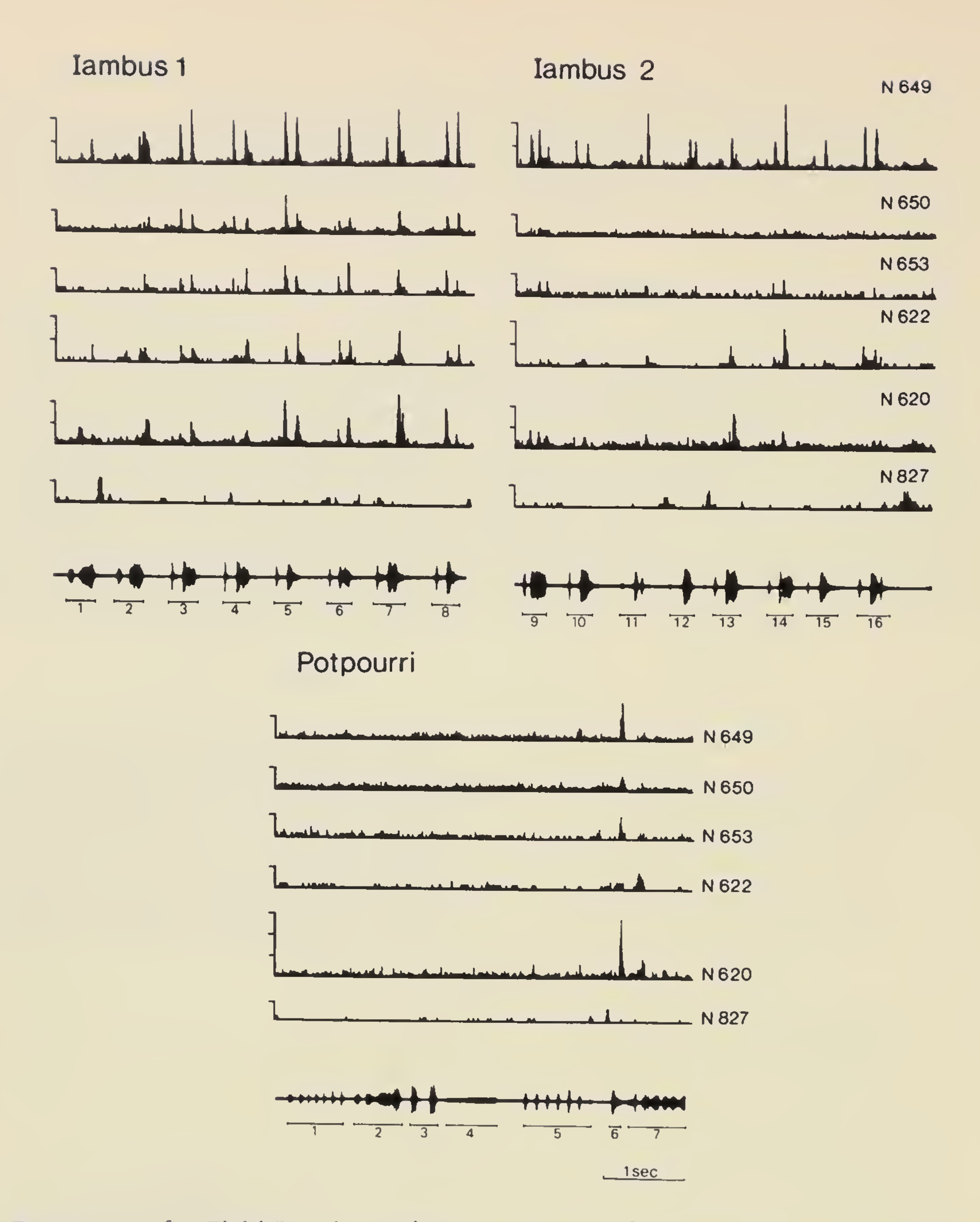


FIGURE 3. Responses of 6 Field L units to the presentation of 16 natural variations of the Iambus (Iambus 1 and Iambus 2) and to a Potpourri of 7 other vocalizations of the Guinea Fowl including Kecker (lower sound track 2 and 3) and Iambus type calls (sound track 5 and 6). There are only responses to Iambi and Iambus type calls. Most units respond to a high number of Iambus variations.

harmonics. This typical combination of spectral components is called the Focal Property of the Iambus (SCHEICH, 1977). Kecker calls are built from higher harmonics of about 300 Hz with more or less additional noise. The two calls have a number of harmonics in common. The energy of both calls is concentrated between 1 and 7 kHz. However, the dominant frequencies, i.e. the strongest energy, of Iambi are between 1 and 2 kHz and those of Kecker between 2 and 3 kHz.

We have concentrated our analysis in the auditory midbrain nucleus (MLD) and in Field L of the neostriatum on neurons which distinguish the Iambus from other calls, particularly from Kecker calls.

More than 90 % MLD neurons which responded to the Iambus gave also responses to Kecker. Among the remaining Iambus-responsive neurons most gave weak responses to Kecker (Fig. 2). Thus, there was a quantitative distinction. Occasionally a

neuron did not respond to Kecker (Fig. 2, N 705) but was excited by other non-Iambus calls of the species.

The low integration level of MLD units is also shown by their temporal discharge pattern. In Fig. 2 most units give multiple bursts of activity throughout the duration of a call corresponding to short spectral or temporal events (compare the discharge patterns of Field L units in Figs. 2 and 3).

The frequency tuning of Iambus-responsive Neurons in MLD was non-uniform. There was narrow tuning with various best frequencies corresponding to particular lines in the Iambus spectrum. Tuning to harmonic combinations of frequencies, as they occur in Iambus and Kecker calls, was seen. Since the two calls have harmonics in common such units did not discriminate between them (SCHEICH et al., 1977).

In Field L 10 % of the Iambus-responsive neurons gave no response to spectrally different calls (Iambus-selective neurons). Thus in contrast to MLD neurons there was a qualitative distinction of the Iambus from other calls (Fig. 3). Neuronal specialization was corroborated by the fact that Iambus-selective neurons as a majority gave responses to more than 8 out of 16 natural variations of the Iambus (Fig. 3, Iambus 1 and Iambus 2). The tuning analysis showed that these neurons preferred frequencies or frequency combinations within the 1 to 2 kHz band which corresponds to the dominant frequencies of the Iambus. A high sensitivity was seen to synthetic spectra which mimicked the Focal Property of the Iambus (see above) and had spectral peaks between 1 and 2 kHz. Iambus-selective and -responsive neurons were found concentrated in a 1 to 2 kHz subarea of the tonotopically organized Field L (BONKE et al., in prep.).

This comparison of midbrain and forebrain neurons in the Guinea Fowl allows the conclusion that auditory pattern recognition is primarily a function of neurons at the forebrain level. Forebrain neurons appear to recognize the Iambus because of their sensitivy for the characteristic wide-band spectrum of this call with a spectral peak which is different for other wide-band calls with a similar spectrum.

Acknowledgement

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Response Selectivity of Auditory Forebrain Neurons in a Songbird

Hans Joachim Leppelsack

The problem

A principal function within the avian central nervous system must be to recognize biologically significant sounds within the individual's acoustic environment and initiate appropriate behavioral responses. The neural analysis of biologically significant sounds necessitates an understanding of how the single elements within various levels of the auditory pathway respond to these stimuli. The afferent avian auditory pathway extends from the receptor cells in the inner ear, through several nuclei located in the medulla, mesencephalon, diencephalon and at least as far as the field L in the telencephalon (Boord, 1969). This general scheme is similar to the ascending auditory pathway of both reptiles (Pritz, 1974) and mammals (Merzenich et al., 1977). Contrasting models for information processing in the auditory pathway of higher vertebrates (Bullock, 1977) have basically considered hierarchial or parallel processing concepts to be the basis for central nervous auditory analysis. Irrespective of the type of model favoured, there should perhaps be some systematic development of information processing from the lower to higher centers. This development may be represented by some progressive change in auditory responses by single neurons within the auditory pathway. Recordings from neurons of the highest centers, for example, may reflect all of the analytical processing that has occurred in lower centers and be close to the final result of the analysis. By adapting this idea the present experiments were recorded from single neurons in the Field L. This is the highest known center in the afferent auditory pathway of birds (Karten, 1968) and is in close anatomical proximity to the hyperstriatum ventrale pars caudale (HVc), an important center of the descending vocal pathway of birds (Nottebohm et al., 1976).

It is possible that information processing within higher order auditory neurons has developed either by a reduction of information that a neuron receives about a particular sound, or by a change in information about a specific sound structure to which a neuron may respond. We have developed research methods to assess whether qualitative or quantitative response differences emerge in the auditory pathway.

The research strategy

The overall research strategy has been 1) to initially develop a quantitative method for measuring the response selectivity of auditory neurons and apply this method to neurons of the Field L, 2) to apply the same method to neurons close to the input of the auditory pathway i.e. the cochlear ganglion, 3) to compare and contrast response selectivity at both these centers. Based on the results of the quantitative method it is then possible, 4) to describe qualitatively (modulation analysis) the characteristic response features of auditory neurons in both centers, 5) to compare such an analysis at both centers as an indication of the analytic strategy in the auditory system, 6) to compare

Lehrstuhl für Allgemeine Zoologie der Ruhr-Universität Bochum, 4630 Bochum 1, Bundesrepublik Deutschland.

the neuronal response limits with the natural variability of specific sounds, in order to establish the neural "acuity" of sound detection.

Selectivity of Field L neurons

Previous studies of Field L neurons in the awake Starling (Leppelsack & Vogt, 1976; Leppelsack, 1978) have demonstrated a very high selectivity of these neurons to acoustic stimuli. In these studies auditory units were recorded with glass micropipettes (3M NaCl). A stimulus program was used consisting of a sequence of natural sounds which represent the typical vocal repertoire of the Starling. This sequence was presented several times to each neuron and the number and types of response was determined. Judgement of the selectivity of a neuron to the natural sounds was based on the ratio between the number of sounds evoked a response and the total number of sounds presented in the program. Similar approaches have been made in order to describe the selectivity of neurons within the auditory cortex of the squirrel monkey (Winter & Funkenstein, 1973; Newman & Wollberg, 1973).

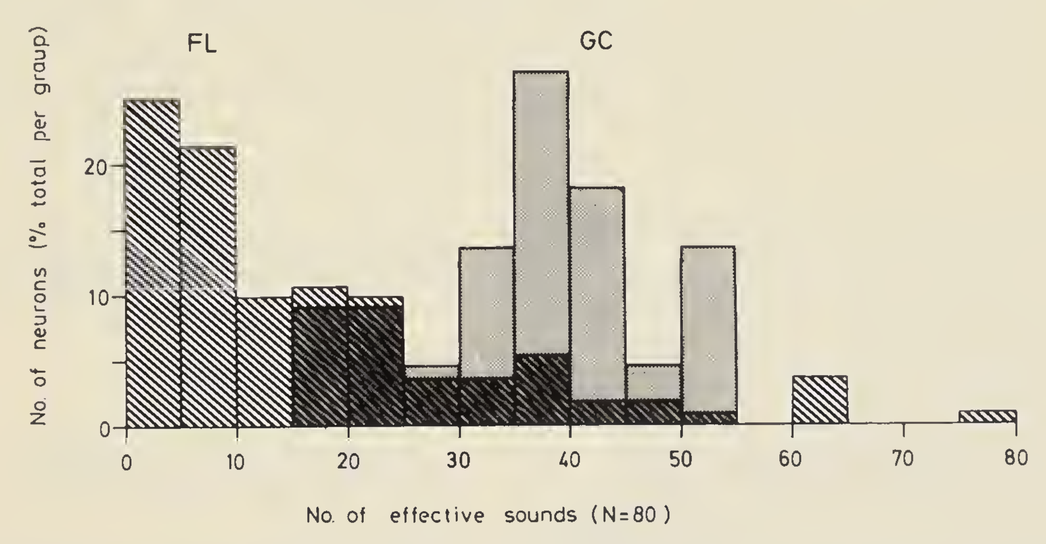


Figure 1. Distribution for degree of selectivity of neurons in Field L (FL, hatched columns) and of ganglion cochleare (G., stippled columns) based on a sequence of 80 different Starling sounds.

The results of the present study are shown in Fig. 1. The hatched columns show the selictivity of the neuronal population of Field L. It can be seen that most of the neurons respond to only a few sounds, in fact more than 50 % of all units respond to less than 15 out of the 80 sounds presented, while only 10 % respond to 40 or more different sounds. There are several neurons that respond only to one natural sound and show no responde to pure tones at all. Even in these highly selective neurons the present method of analysis does not allow an extensive judgement about the response characteristics since further stimulus control will be necessary to determine the limits (e.g. stimulus modification). Nor do we have any evidence that these highly selective neurons have a detector function.

Response selectivity at different levels of the auditory pathway

Neurons in the periphery of the auditory pathway have been investigated (cochlear ganglion) in the anaesthetized Starling (Manley & Leppelsack, 1977; Leppelsack & Manley, 1978). These neurons were stimulated with the Starling vocalization stimulus

program (as above) and their responses were analyzed in exactly the same way as for Field L neurons. The results of these experiments are shown by the stippled columns in Fig. 1. More than 50 % of the neurons in the cochlear ganglion responded to 31—45 out of 80 possible sounds. Thus the responses of ganglion cells appear to be noticably less selective than that exhibited by Field L neurons. The higher selectivity of forebrain neurons, judged on this basis, would seem to be a direct result of central nervous processing. There is some evidence that these results are not simply due to anaesthesia.

Approaches to the mechanisms of selectivity*

Neurons in the periphery usually appear to act as simple frequency filters, according to their tuning curve (LEPPELSACK & MANLEY, 1978). However many Field L neurons, especially those that are the most selective and perhaps the most interesting do not respond to pure tones. Even less selective neurons of the Field L do not necessarily have predictable responses to natural stimuli based on a pure tone analysis. Therefore, to test the functional properties of such neurons a computer-aided method has been developed, the modulation analysis (MA), which does not depend upon using simple sounds as stimuli (DÖRRSCHEIDT, 1973, 1977, 1978). The MA resolves species-specific sounds into time courses of amplitude and frequency (see Fig. 2). The frequency evaluation is

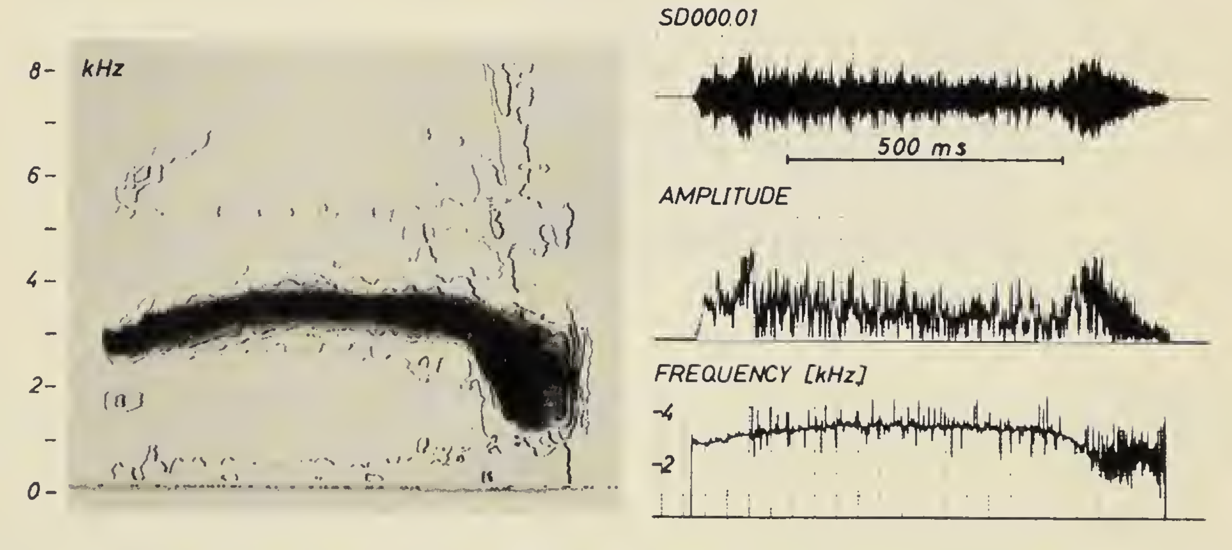


FIGURE 2. Contour sonagram and modulation analysis (MA) of a Starling whistle (data set: SD000.01). Compare the similarity of the sonagram and the frequency course evaluated by the MA technique.

based solely on the zero crossings contained in each sound, similar to GREENEWALT (1968). The present procedure, however, is a reversible one, enabling frequence and amplitude data to be used to reconstruct the original sound. An important point is that before this resynthesis, modifications can be made to each set of data independently. This permits extensive latitude in controlling the time function of amplitude and frequency for any given sound modification. Possible modifications include changes in the frequency and amplitude range, frequency bandwidth and time duration. Such modifications can be introduced either for the complete sound sequence of vocalizations or in

* The following experiments were performed in cooperation with Dr. G. J. DÖRRSCHEIDT (Lehrstuhl für Allgemeine Zoologie, Ruhr-Universität Bochum), who contributed the modulation analysis technique and important ideas concerning the stimulation strategy.

any single element. Thus the response characteristics of Field L neuron have been retested as follows. Initially the natural sounds to which a neuron responds are determined. Then, by using the computer resynthesized set of sounds, in which the time functions of frequency or amplitude of the natural sounds have been systematically altered the neuron is retested. The characteristic response limits for individual neurons were defined by the sounds within the modified stimulus range to which there was no response. Preliminary results obtained through the use of this method are based on an initial sample of 74 neurons.

Effects of sound modification on the response of single neurons

The following examples will show some applications of the sound modification technique in Field L neurons. In this paper only simple operations on the structure of one Starling sound are performed. The alteration of frequency produced by multiplying every instantaneous frequency value by a constant factor (0.8 or 1.2) can lead to pronounced changes in the response pattern of a single neuron. Besides gradual differences in the response amplitude, there can occur changes in the response pattern, for example from excitation to inhibition and from on-excitation to off-excitation. A change of stimulus amplitude components usually does not cause any dramatic effects.

Profound effects on discharge properties can be produced by changes in the temporal pattern of the stimulus. The simplest change, by time inversion of the sound, can influence a response strongly (see Fig. 3). Only in rare cases does an inversion of the neuronal response pattern resemble that of the sound pattern. Such a response pattern would be expected in neurons which behave simply as frequency filters and can be anticipated for neurons in the cochlear ganglion (LEPPELSACK & MANLEY, 1978). Neuron CA 25-4-6 in Fig. 3 shows this rarely observed "frequency filter" behavior. In most of the other neurons studied there has been either a very distinct change of the response, as in D1-12 (Fig. 3) or only one direction of time course causes a response. Curiously, neuron D1-13 responds only to the unnatural time course.

Another effective sound modification in the time domain can be a change in sound duration. Using the present method this can be changed without altering the frequency course of the sound. This procedure especially affects neurons that respond to dynamic changes within the sound pattern. i.e. the dynamic changes are either accelerated or

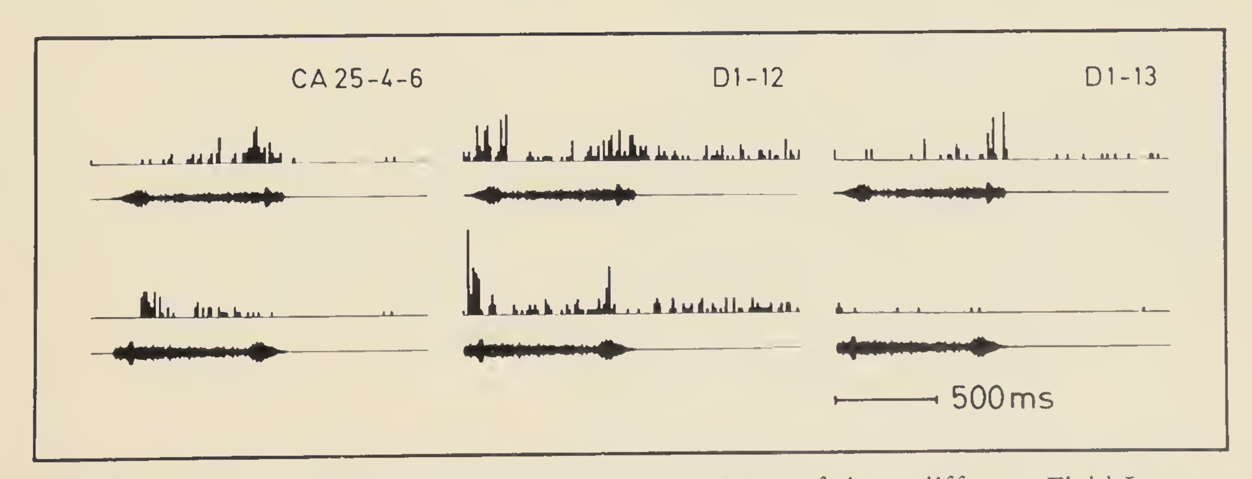


FIGURE 3. Responses (peri-stimulus time histograms, PSTH) of three different Field L neurons to the original sound (lower) and a time inversion modification (upper). Note the different degree of stimulus selectivity in the responses of these neurons.

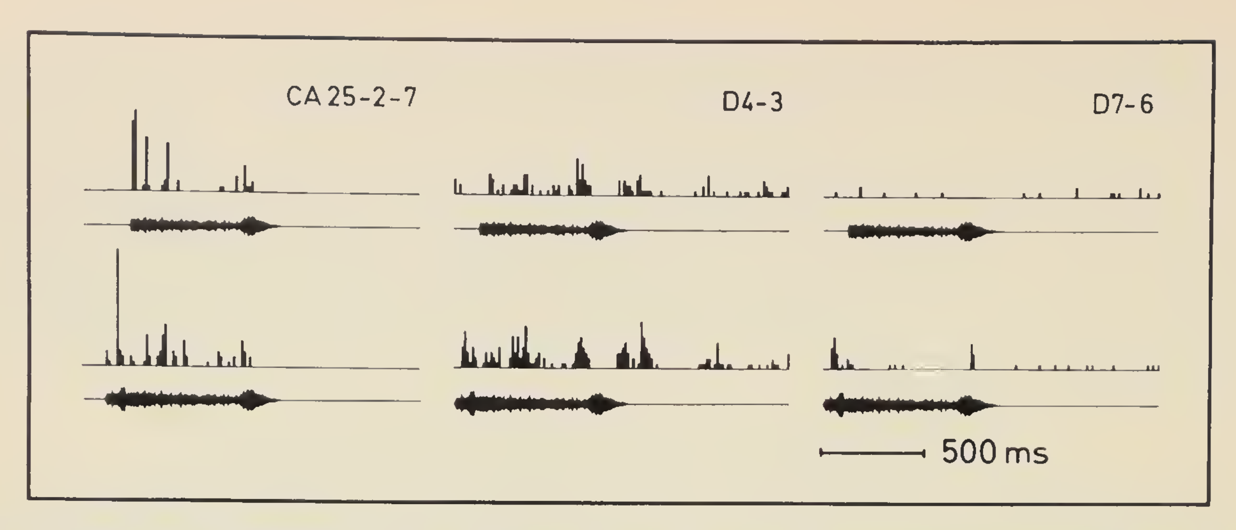


FIGURE 4. Responses (PSTH) of three different Field L neurons to the original sound (lower) and a modification with the initial section removed (upper). Note the specificity of response in Neuron D7—6.

retarded. The dynamic response of a neuron can be influenced in different ways, and normally an accelerated rate of change causes a stronger response.

The importance of the temporal pattern of a sound can also be demonstrated by removing sections of the sound and comparing the neuronal response to that of the original. In Fig. 4 the responses of three neurons are shown. The stimuli consists of the original and a version in which the initial section is removed. The neurons CA 25-2-7 and D4-3 show a change of amplitude (spikes/bin) within different parts of their response. Neuron D7-6 does not respond at all when the initial section of the sound is removed, but afterwards it responds again to the original sound. Such a response can be considered as another obvious example of the influence of acoustic time patterns on the responses of Field L neurons. It can be suggested that in the higher centers of the auditory pathway of birds, the temporal pattern of the sound probably plays an important role.

Analysis of neuronal response behavior

Fig. 5 shows the responses of two neurons, each of which was stimulated by 12 different sound modifications and the original sound (see Fig. 2) both before and after the modifications; each different modification is described in the caption of Fig. 5. The neurons shown here provide examples of very unselective (D12) (D12) and highly selective (D9) neurons within the Field L.

Neuron D12 responds at the beginning and near the end of the test sound with phasic excitation. Both responses occur during parts of the sound stimulus in which amplitude and frequency change simultaneously. The neuron responds over a wide range of frequencies (Fig. 5: D12, No. 6, 7, 9), but the shape of its response pattern is frequency dependent (6, 7). The early response component is almost totally unaffected when given a sound stimulus of constant frequency or amplitude over its entire duration (3, 4). Increasing the stimulus frequency by a factor 1.2 (7), deleting the initial part (9), or linearizing the frequency course (8), also fails to affect the early response. However, the early response is changed by lowering the stimulus frequency by a factor of 0.8 or by time course inversion (5). Reducing the stimulus duration, i.e. by shortening the rise-time, serves to reduce the early response as well. In the cases of time contraction

(T/2) there is a minimal response and also at T/3 the response is smaller than the original. In this neuron the late response is easier to affect and it only remains unchanged if the initial section of the sound stimulus is removed (9) or when the frequency is linearized (8). The late response becomes stronger when the stimulus frequency is raised by a factor of 1.2 (7) and the response pattern is altered by time inversion (5). Furthermore, the response diminishes or even disappears when the middle section of the sound has been deleted (10) or when either the stimulus duration has been reduced (12, 13) or the stimulus frequency is lowered by a factor of 0.8 (6). From this response profile and the sound stimuli characteristics (Fig. 2) it can be concluded that this particular neuron (tested at an sound pressure level of 70 dB) indicates an on-response in the frequency range of 1.5—4.0 kHz, which is consistent with the tuning curve. In addition this neuron prefers a slow rise-time and will respond to a constant frequency below 3.0 kHz. With a constant frequency between 3.0—4.0 kHz it can be driven by a combination of rising amplitude and falling frequency. Finally, neuron D9 only responds to the time inverted version of the original sound (Fig. 5: D9 No. 5). All other modifications, including even the original sound, did not cause the neuron to respond. The characteristics of this response behavior seem to indicate that the neuron responded only to fast rising frequency modulation in a range below 3.0 kHz.

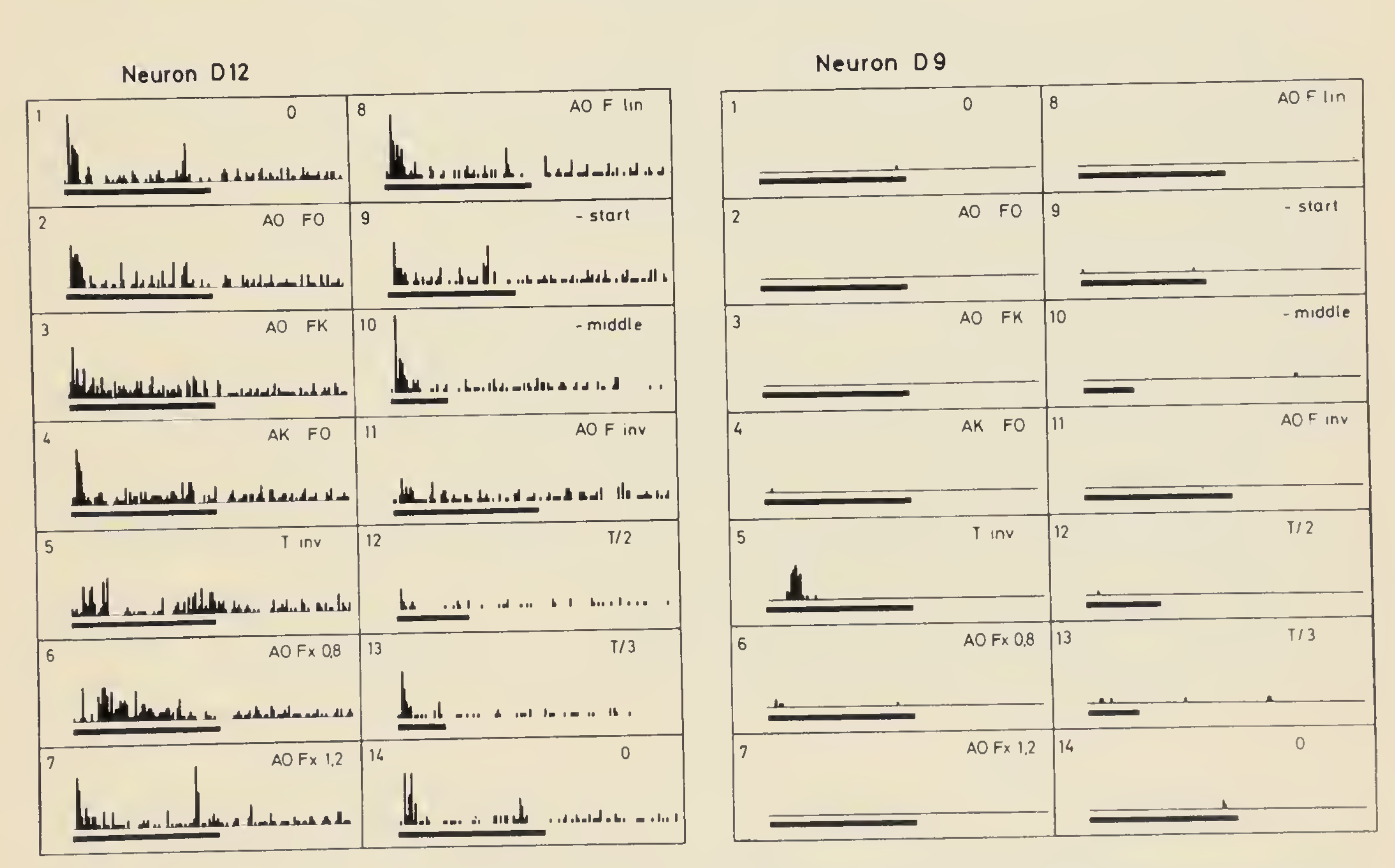


FIGURE 5. Responses of two Field L neurons (D12, D9) to the same set of test sounds consisting of two originals (No. 1 and 14) and 12 different modifications. Abbreviations: O = original; A = amplitude; F = frequency; K = constant; T = time; inv. = inverted; lin. = linearized; — start = initial section removed; — middle = middle section removed. Amplitude and frequency time course as defined by MA.

Conclusions

These preliminary results indicate examples of extremely selective auditory neurons and also neurons with complex but inherently unselective responses. Even these unse-

lective neurons show distinct differences from the responses of peripheral auditory neurons in the cochlear ganglion. Thus neither a strictly hierarchical or strictly parallel processing system can be totally supported at this time. It is felt that the modulation analysis method described here will be an extremely useful tool in delimiting the response criteria for selectivity of auditory neurons. This may be particularly applicable when step-wise modifications of species-specific sounds can be produced during the experiment. These additional modifications can be based on the results of an initial test of the response properties, here for Field L neurons in the bird. Such an approach is now being used in current experiments.

Acknowledgements

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SYMPOSIUM ON ECOLOGY OF VOCALIZATIONS

6. VI. 1978

CONVENERS: G. THIELCKE AND C. CHAPPUIS

The Ecological Background for the Evolution of Vocal Sounds Used at Close Range

Eugene S. Morton

Introduction

While the physical structure of long range sounds, e.g. most bird song, may be influenced directly by habitat acoustics (Chappuis, 1971; Morton, 1975), short range sounds are only indirectly related to ecological factors, if at all (Morton, 1977).

This paper discusses ecological factors and social factors that influence the physical structure/information component of close range sounds. The direct relationship between a sound's structure and its information has been discussed elsewhere (Morton, 1977). Sound structures that are low and harsh indicate the sender's aggressive tendency; sounds that are high and tonal indicate the sender's fearful or appeasing state. These sounds form endpoints of a continuum. The endpoint sounds function to increase or decrease the distance between sender and receiver(s) during agonistic or sexual behavior or interactions with a predator. Sounds intermediate to these endpoints whose frequencies rise or become more tonal relate to the sender's relatively more appeasing or fearful state whereas sounds that decrease in frequency or become harsher indicate a more aggressive state. These sounds function in a wide variety of social encounters but often cause subtle or no obvious reaction in receivers. Sounds with a rising and falling frequency indicate something of interest has been perceived. These often function as alarm notes or contact notes in social species and may be used in intraspecific agonistic behavior but not during overt aggression. The central assumption here is that sound structure is not arbitrary in relation to the information but follows the code as outlined above and explained more fully in Morton (1977). Using this as a base, we will try to show how ecology and social systems work synergistically during the evolution of close range sounds. At the same time, we will focus in on both these ecological factors and sociobiological or genetic arguments to attempt an explanation of communication differences and similarities within a New World genus of passerines, the *Thryothorus* wrens.

Ecological component

General Considerations

In tropical passerines there is a close relationship among mating system, food, and territorial behavior. Nearly 65% of Panama's lowland passerine species are monogamous, permanently pairbonded, and permanently territorial (pers. obs.). All of these primarily eat insects, a resource contained within areas small enough to be defendible and available continually in tropical latitudes.

That permanent pair-bonds and territorial defense co-occur as the predominant system in these birds argues strongly that permanent pair bonds will be favored by selection if pairs are more successful than individuals in defending territories. Because being successful

Smithsonian Institution, Washington, D.C., U.S.A.

always must equate to breeding success, the size of these permanent territories must include nest sites (quite specific in many tropical species), and enough food to feed the adults and their young. This combination of factors suggests why female participation in territorial defense is so characteristic of tropical passerines: it is to her advantage to "help" the male maintain a territory size larger than he could defend alone since this leads to her increased reproduction. Duetting by the bonded pair is often the manifestation of the female's participation in territorial defense (WICKLER & SEIBT, 1977; pers. obs.).

The general ecological component that is important in the evolution of social relations and communication to the majority of the world's passerines is a dispersed, cryptic, food resource whose availability is best predicted by habitat structure (see also SNOW, 1971). Competition, especially intraspecific competition, has overlaid the permanent pair-bond onto this ecological background. But a detailed look at related species that share this general ecological component shows extensive variation in sex roles and communication that are difficult to explain using only ecological criteria.

Thryothorus Wrens

Of the 11 *Thryothorus* wrens found in Panama we will focus on 4 species that occur together on the Canal Zone's Pacific slope. Table 1 shows some qualitative information about their ecological divergence, but all 4 species may be captured in a single mist net placement. All feed on insects from 2 to 50 mm obtained by probing, gleaning, and leaf tossing. *T. leucotis* has both the highest numerical density and most restricted habitat. It favors non-forested brush covered with vines, generally seasonally flooded areas or along river edges. The other 3 species co-occur in shrubby undergrowth of seasonally dry woods. Only *T. rufalbus* co-occur with *T. leucotis* on the Pacific coast but it is often attacked by the latter and even responds to playbacks of the different *T. rufalbus* song. In northern Venezuela, *T. leucotis* occurs alone in gallery forests, perhaps a consequence of this interspecific aggression.

Social component

Using playbacks of duet songs, natural field observations, and studies of caged birds, we have obtained the data in Table 1. The species are arranged from left to right in order of increasing female participation in territorial defense. We point out that the species-specific structure of the duet song and the frequency of female participation in duetting correlates with an array of intra-pair behaviors. In *T. leucotis* one cannot tell the female and male portions of the songs apart, either sex may initiate a duet, they always sing side-by-side, and rarely does either sing alone. They also forage together and continually allopreen when resting. In decided contrast, *T. rufalbus* males respond alone (>80% of observations, N = 45) to a playback of a duet, the female's song is higher pitched than the male's and is simultaneous but not antiphonal and they do not sing side-by-side often. They forage separately and engage in frequent intrapair aggression with the male dominant and they do not engage in allopreening.

Thus in *T. leucotis* we have near equality in territorial defense, care of young (parental investment), and size: sex roles are nearly the same. In *T. rufalbus* sex roles and sizes have diverged with males taking a territorial defense burden, females a large parental investment.

TABLE 1: A comparison of behavioral and ecological characteristics of *Thryothorus* wrens.

	rufalbus	*fasciatoventris*	*rutilus*	*leucotis*
Social behaviors				
allopreening	none	frequent	frequent	very frequent
intrapair aggression	frequent	?	?	none
Territory defense				
female participation	occasional	occasional	frequent	obligate
synchrony of duets	simultaneous overlay	simultaneous overlay	loose antiphonal	tight antiphonal
Parental care				
feeding the young	only ♀	?	?	both ♀ & ♂
retention of young	not beyond breeding season	?	not beyond breeding season	2–3 months after breeding season
Sexual dimorphism				
color dimorphism	monomorphic	monomorphic	monomorphic	monomorphic
weight ♂–♀	28.8 23.7	30.1 24.4	18.0 16.5	21.6 19.4
% size dimorphism	18.8%	18.9%	8.3%	10.4%
Foraging				
preference	on ground low vine tangles	canopy to low vine tangles to ground	subcanopy vines underside of canopy	subcanopy vines
mates forage together?	no	no	frequently	always
Abundance	moderate	low	moderate	high

We hypothesize that these differences are driven only indirectly by ecological differences that operate chiefly through differences in intraspecific competition. *T. rufalbus* is a habitat generalist and is less densely spaced when compared with *T. leucotis*. In *T. leucotis*, this high density has selected for efficient territorial defense, i.e. cooperation between the pair members to the point that they have become one 40g fighting unit rather than two birds that reflect genetic self-interest through divergence in their roles. This ecological background is important but may act more as a catalyst to produce an array of behaviors more directly related to intraspecific competition. It is significant that only *T. leucotis* characteristically retain fledged young until the food scarcity of the dry season begins and that these young participate in territorial defense.

The role of ecology in the evolution of close-range vocal sound structure

We discussed differences in duet song structure that correlate with an array of social behaviors, but how do these structures relate to the motivation-structural rules mentioned before and how are the structures and their function related? When a *T. leucotis* pair detect an intruder the birds incorporate high tonal seet sounds into the coordinated duet. These seets precede each duet and are also used outside the context of territorial defense as

appeasement. In contrast, *T. rufalbus* pairs do not incorporate appeasing sounds in their duets but these pairs infrequently join together for territorial defense. This comparison shows the adaptiveness of *T. leucotis* duets: appeasing close-range sounds and loud antiphonal long calls that together function to reduce aggression between the pair members in a situation where their cooperation benefits both.

Another close contact call, the pi-seet is used by all *Thryothorus* species so far studied (8 species) and by *Thryomanes bewickii* but by no others (9 genera).

The call's structure is variable in pitch and in the emphasis given two elements. The seet element may be used without the attention-getting pi- when the calling bird is close to the receiver. In all species studied except the temperate zone *T. ludovicianus, T. leucotis,* and *T. rutilus* this call is restricted to fledged young before they become independent. As the motivation-structural rule predicts, this call signifies low aggression or "friendliness" and functions to permit close contact. In the two tropical species that retain this call in the adults, frequent mate contact in foraging is characteristic. In *T. ludovicianus* females duet only during fights with other pairs, not in long call (song) territorial maintenance (Morton & Shalter, 1977). Since their duets function only in close contact fights (and are therefore not adapted for long distance propagation) the female uses a harsh, rapidly repeated series of short notes. But pi-seets are used by both male and female *T. ludovicianus* to maintain close association that is a prerequisite for efficient joint territorial defense.

The ecological background that permits high populations and the resultant intraspecific cooperation that selects for pair cooperation in territorial defense appears to have overcome the more normal conflict of genetic interest between the sexes (Trivers, 1972).

The motivation-structural rules and deceptive communication

We believe that signal structure is tightly linked to motivation as the result of the ease that sound can be used for deceptive purposes. The prevalent interactional approach has emphasized the role communication has in producing efficient social interactions but has led away from consideration of the disadvantage of vocal communication as an evolutionarily stable entity. If vocal communication could be easily used deceptively such that information in the selfish interest of the sender is detrimental to the receiver if it is attended to and used, then selection would not favor vocal communication.

Nonetheless, vocalizations that are deceptive can remain in the vocal repertoire if they function to produce benefits for receivers. An example might be the chevron-shaped chips used by *Parus* species. A functional approach states that these serve as "contact" notes to keep flock members together. The motivation approach says that the information conveyed, something "of interest" has been perceived by the sender, benefits the sender by slowing down the flock's movement or causing movement toward the sound.

The ecological component in the evolution of close-range sound structures can be assessed: if resources are sufficiently rich responding to chips is of benefit in the trade-off between loss of foraging time and the benefits to being a flock member and the chip will remain to appear to us to be a contact note. However, if we only study a sound's function we will never be able to assess communication in terms of individual selection nor to understand why so many sound structures are used in many different contexts.

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The Effect of Sympatric Relatives on the Evolution of Song

R. Neil Brown and R. E. Lemon

Introduction

A great deal of research and speculation have been directed towards explaining the diversity and complexity of acoustic signals produced by birds. There are many determinants of song form in any particular species and these determinants may be either selective or non-selective. Non-selective or stochastic influences have not been well studied, but the existence of dialects, improvisation in song development of young birds, and imprecision in the copying process whereby young birds learn their parents' songs, all argue for a certain stochastic element in the evolution of song form.

There are a number of non-stochastic determinants of song form. For example, some constraints on song form must result from the physical dimensions of the sound producing apparatus of the species (Konishi, 1970; Greenewalt, 1968). Form of signals is also influenced by their function. For example the distance over which communication is required and whether or not the sender need be accurately located by his signal may affect signal form (Marler, 1959; Wiley, 1976).

Physical attributes of the environment are also important in the evolution of species signals and may be either physical (structural) or acoustic in nature. Physical characteristics of habitat such as foliage and obstacles have been shown to be important in the selection of frequency ranges of species songs (Ficken & Ficken, 1963; Chappuis, 1971; Jilka & Leisler, 1974; Morton, 1975).

The acoustic environment of a species has also been proposed as an important determinant of song structure. In particular, the presence of other species and their acoustic signals may affect the form of any given species song (Lack & Southern, 1942; Marler, 1960). Instances of both convergence and divergence of song between sympatric species have been proposed.

Cody (1969, 1974) proposed that convergence of song characteristics might occur between closely competing species in order to facilitate interspecific spacing and gave a number of examples of such convergence. However, Brown (1977) suggested that important evidence was lacking in many of the proposed cases of song.

Two allied hypotheses have been used in relation to divergence between songs of sympatric species. These are "contrast reinforcement" and "loss of contrast". The contrast reinforcement basically states that "natural selection is responsible for the establishment of isolating barriers" (Mayr, 1963: 548). Thus, when newly-formed species come into contact, selection against hybridization will result in increasing distinctiveness of isolating mechanisms such as song. Similarly, one might expect selection against similar territorial defence signals where two newly-formed species had evolved ecological differences.

The argument underlying loss of contrast is closely related to that of contrast reinforcement. Loss of contrast assumes that when species move into areas where the sound environment is less complex (e. g. islands), they may be relieved of previous selection for

First author's adress: Trent University, Peterborough, Ontario, Canada

distinctiveness and may evolve songs which are either more variable or more like their ancestral songs. THIELCKE (1969, 1973) has reviewed the literature on both contrast reinforcement and loss of contrast in song and concluded that there is as yet no solid evidence for either of them.

In this paper we give evidence that contrast reinforcement exists between songs of species of *Thryothorus* wrens. We discuss the nature of differences between sympatric species of *Thryothorus* and propose that "strategies" of singing may recur in allopatric species.

The Genus *Thryothorus*

The genus *Thryothorus* appears to be an excellent group in which to study the evolution of song form, and particularly the influence of sympatric relatives. This genus of wrens is widespread through the Neotropics, has achieved considerable species diversity (over 20 species), and presents a considerable array of allopatric-sympatric combinations. *Thryothorus* species rely heavily on acoustic communication due to the nature of their habitat, and their territorial songs are reasonably distinct and simple in comparison with many families of birds.

Thryothorus sinaloa and *T. felix*

Elsewhere (BROWN & LEMON MS), we have described in detail the song characteristics of *Thryothorus sinaloa* and *T. felix.* The two morphologically similar species are sympatric over a large area of western Mexico. We found a number of striking differences between the two species in the structure of song units, patterning of song bouts, and in duetting behavior. The extensive nature of these differences appears to exceed the difference required simply for species recognition. Species recognition could conceivably be achieved through a small number of parameters with low intraspecies variability.

Elsewhere (BROWN & LEMON MS) we discuss the use of measures of song parameter variability in making inferences concerning species recognition factors. We argue that although our species of wrens must contend in an evolutionary sense with a wide range of species songs, it is reasonable to assume a priori that there is more potential for acoustic confusion among *Thryothorus* species than between a *Thryothorus* species and any other sympatric species. Thus in looking for possible effects of acoustic environment on song form, we have limited our study to members of the same genus.

"Strategies" of singing

As a follow-up to our study on *T. sinaloa* and *T. felix,* we did some analysis of singing behavior of two further *Thryothorus* species, *T. pleurostictus* and *T. maculipectus.* This work brought a somewhat surprising result. The songs of *T. maculipectus,* a more southerly geographic replacement of *T. felix* sounded very similar to songs of *T. felix,* while a less striking similarity was also noticed between the songs of *T. pleurostictus* and *T. sinaloa* whose ranges are also more or less contiguously allopatric.

A cluster analysis of the four species mentioned along with a fifth species, *T. ludovicianus* (allopatric from all the others), confirmed our impression that the songs of *T. maculipectus* and *T. felix* were similar, as were those of *T. sinaloa* and *T. pleurostictus.*

We based the cluster analysis on nineteen different parameters of song including five counts, five temporal measures and nine frequency parameters. Cluster analysis was done using WARD's method (error sum of squares) (WISHART 1975). Greatest differences of song were found between sympatric species pairs, as predicted by the contrast reinforcement hypothesis.

Even more interesting than the similarity of songs of geographic replacements were the parallel differences in other features of singing behaviour which we noticed. *T. felix* and *T. maculipectus,* with their short songs and few syllable repetitions in songs, both sang highly repetitive song bouts, and both species used their songs in male-female duetting. *T. sinaloa* and *T. pleurostictus* on the other hand, with long songs and many syllable repetitions, sing bouts of high immediate variety, and do not sing male-female duets.

These findings led us to the notion that song "strategies" might occur in the genus, with certain types of song form being correlated with other features of singing behaviour. Our grouping of characteristics into singing "strategies" has analogies in the practice of grouping characteristics into reproductive strategies or life history strategies. Extremes in singing strategies are represented by strategies 'A' and 'B' in Table 1.

TABLE 1: Strategies of Singing in *Thryothorus.*

	Strategy 'A' eg felix	Strategy 'B' eg sinaloa
Song Form		
Song Length	Short	Long
Internal Repetitions	Few	Many
Syllable Length	Long	Short
Frequency	High	Low
Syllable Slope	Low	High
Song Bouts	AAA···BBB···	ABC···ABC···
Duetting	Present	Absent

Shown are extremes in singing strategies which we have labelled Strategies A' and 'B'. These extremes would be represented by species such as *T. felix, rutilus,* and *nigricapillus* for Strategy 'A' and *T. sinaloa, rufalbus,* and *pleurostictus* for Strategy 'B'.

In elucidating the nature of song strategies we looked for correlations among various song parameters within the group of ten species of *Thryothorus* we examined. We found a high degree of correlation between a number of parameters of song form in the genus, some of which are illustrated in Table 1. Although we have no direct evidence, we suspect that some correlations of song form parameters are simply a result of the physiology of sound production. Other correlations may result from functional considerations of communication. For instance it is generally believed that both variety and redundancy are required characteristics in a communication system such as singing in birds. Elsewhere (BROWN & LEMON MS), we speculate that these ends may be achieved by different means in *T. sinaloa* and *T. felix.*

Strategies of singing may also be somewhat analogous to adaptive complexes of genetically determined characteristics, and may arise in a similar manner, despite the fact that song is for the most part learned. During the period of initial contact of newly formed species with close relatives, what might well be relatively small differences in song will tend to be emphasized as expected by contrast reinforcement. A significant change in only one parameter (presumably one which is important in species recognition) may lead in turn to concomitant changes in other parameters due to physiological considerations or functional considerations as mentioned above. In turn, these changes in basic song form may lead to other changes in singing behaviour including the patterning of bouts, and the presence or absence of duetting behaviour. The net result is a difference in singing behaviour of sympatric species far in excess of what one might expect simply for species recognition.

Although we have no evidence as yet, it is possible that the direction of initial changes in song of newly contacted species (and thus the ultimate song strategy of the species) may be correlated with ecological differences between species. Our initial study of *T. sinaloa* and *T. felix* showed that considerable differences existed between the species in singing and foraging locations, in their mode of foraging, and in their nesting characteristics. We are unable to confirm at this time whether or not species sharing similar song strategies with either of these species also share certain ecological characteristics.

Central American *Thyothorus*

To test some of the ideas which arose out of our work with Mexican *Thryothorus,* we have begun to look at a number of Central American *Thryothorus* species. Before travelling to Costa Rica to begin our work on Central American species, we made a number of predictions concerning singing behaviour in the group. We relate a few of our predictions here with some preliminary results.

> Prediction One: Sympatric species should consistently show divergence in their song form as demonstrated through cluster analysis, while highly similar species should be allopatric.

Using songs of species we recorded in Costa Rica and Mexico, and recordings from the Cornell Library of Natural Sounds and the Florida State Museum, we performed a further cluster analysis to show the relationship of songs of the four Mexican species previously mentioned plus six additional species of Central American *Thryothorus* (see Figure 1). These preliminary results are somewhat equivocal possibly due to deficiencies in the data. For example, we sometimes had to use species from several localities in order to get an adequate sample size. The patterns of sympatry among the species are also difficult to unravel since broad overlap does not necessarily mean local sympatry or syntopy.

What is clear from the dendrogram is that the three most similar species, *felix, rutilus* and *nigricapillus,* are all allopatric from one another, as we would expect. Somewhat surprising is the fact that two species, *rufalbus* and *pleurostictus,* both in the group with longer, more internally-repetitive songs, are found sympatrically. The exact nature of sympatry between these two species is not known, and it is known that *rufalbus* differs from the other two members of this group in at least one respect (see Prediction Three). We feel that clearer evidence of contrast reinforcement can be obtained by a community approach in recording all *Thryothorus* species present at a number of localities throughout Central America.

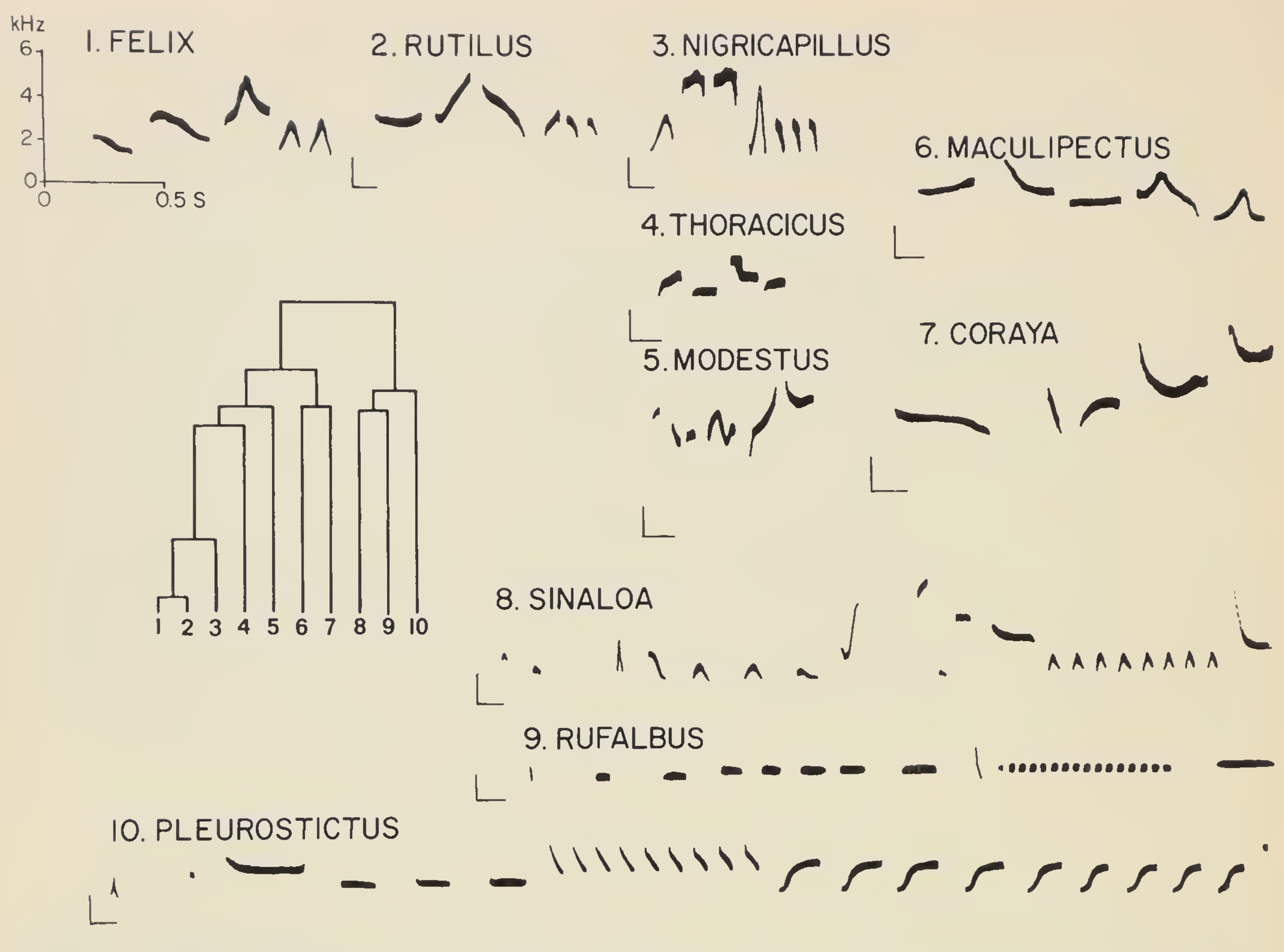


FIGURE 1. Song Relationship of Ten Species of *Thryothorus*. Inset shows dendrogram from cluster analysis by WARD's method (error sum of squares). A minimum of eight different song types for each species were used in the calculations. Seventeen variables of song were used including five counts, five temporal measures, and seven frequency characteristics.

Prediction Two: The correlations of song parameters within the Mexican *Thryothorus* examined should be borne out.

If our idea of strategies of singing are valid we should find similar trends throughout the genus. The results of the cluster analysis do indicate a fairly clear separation between two types of song form, as we found previously in the Mexican species we examined. *T. sinaloa, rufalbus,* and *pleurostictus* are clearly very different from all other species examined. An examination of song parameter correlation in the ten species showed that the same groupings of song parameters are highly correlated as those we found in our previous work on the Mexican species.

Prediction Three: Species having short songs with few repeated syllables should repeat song types many times in succession, while species having long internally repetitive songs should switch song types frequently within singing bouts.

We are able to give a general confirmation of this prediction in that eight of the nine species for which we had at least some long recorded bouts appeared to conform to the prediction (species 1, 2, 3, 4, 5, 6, 7, 9 in Figure 1).*T. rufalbus* did not appear to conform since it possesses a long internally-repetitive song yet gives its songs in repetitive bouts. We have insufficient recordings of *T. coraya* to be able to say which type of song bout it possesses.

Prediction Four: Duetting behaviour should be confined to those species with short songs and few syllable repetitions.

This prediction has been borne out so far in that none of species 8, 9, or 10 has been observed to duet, while duetting has been observed in species 1, 2, 3, 4, and 7.

Conclusion

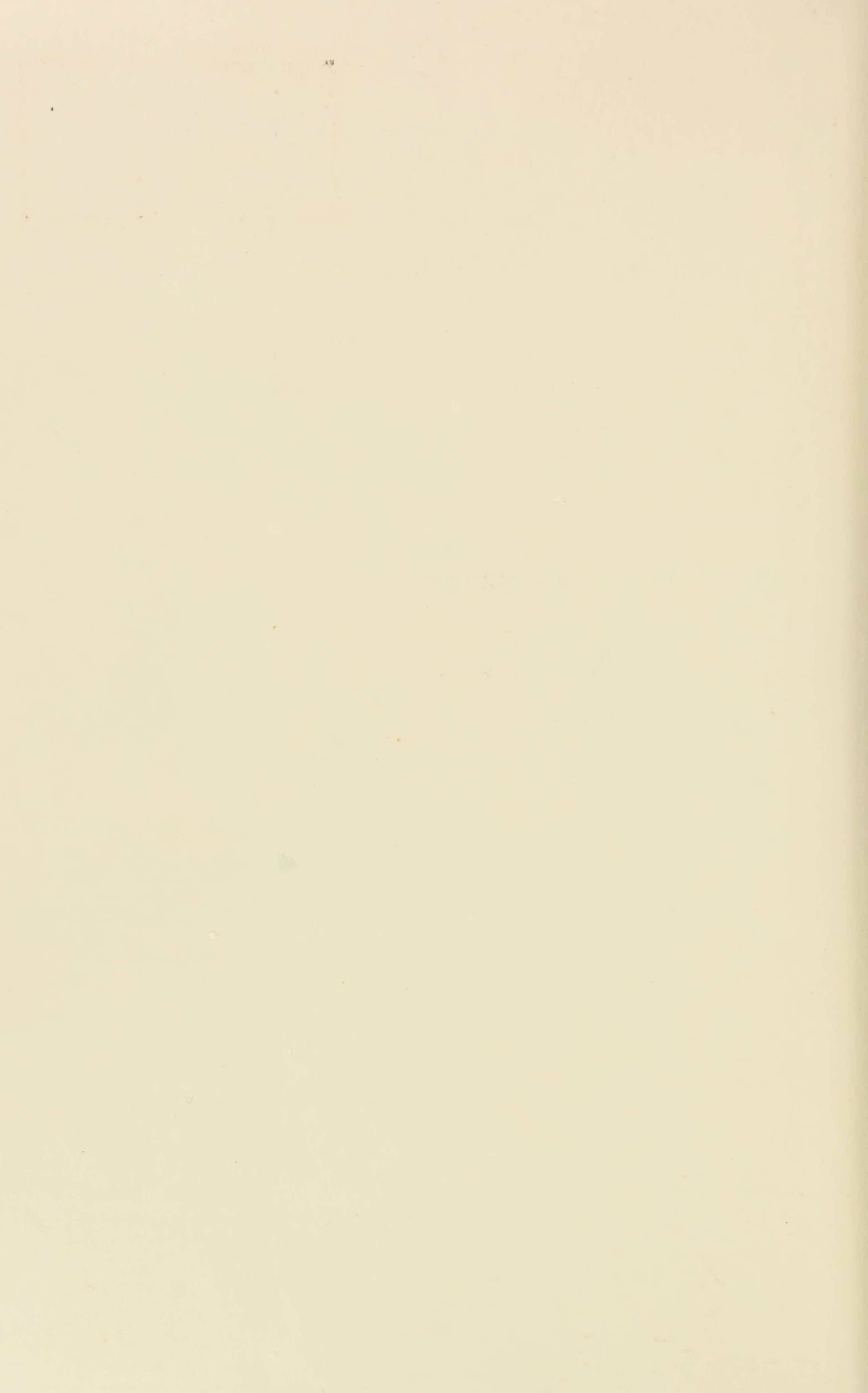
There appear to be strategies of singing behaviour in the genus *Thryothorus* which are represented by two somewhat extreme forms. Strategies of singing may consist of correlated characteristics of song form, bout patterning, and duetting behaviour. Our results from Mexico suggest a tendency for sympatric species to possess very different song form and singing strategies, while results from Central America only suggest that congeners with very similar song form have allopatric ranges.

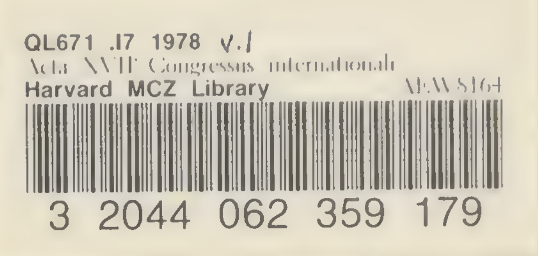
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